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Stock Assessment and Life History of a Newly Discovered Alaska Surf Clam (*Spisula polynyma*) Resource in the Southeastern Bering Sea

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HUGHES, S. E., AND N. BOURNE. 1981. Stock assessment and life history of a newly discovered Alaska surf clam (*Spisula polynyma*) resource in the southeastern Bering Sea. Can. J. Fish. Aquat. Sci. 38: 1173–1181.

A 1977 exploratory survey of subtidal clam resources in the southeastern Bering Sea revealed extensive concentrations of Alaska surf clams (*Spisula polynyma*) along the north coast of the Alaska Peninsula. Using east coast hydraulic clam harvesters, subsequent 1977 and 1978 stock assessment surveys delineated a geographically isolated stock with an estimated exploitable biomass of 329 000 ± 52 000 t and conservatively calculated potential annual yield of 25 017 t (maximum sustainable yield) of whole clams. Production fishing trials at 13 sites in 1978 produced an average catch per unit effort of 815 kg/h with a 1.84-m-wide clam harvester.

Life history studies indicated the species is long-lived (25 yr), slow growing ($K = 0.135$), fully recruited to the spawning population at 8 yr of age, subject to low natural mortality (conservatively calculated as $M = 0.19$), and attains maximum cohort biomass at ages between 9.4 and 13.0 yr. Biological rationale for management measures is presented.

Key words: population assessment, sustained yield, surf clams, Alaska

HUGHES, S. E., AND N. BOURNE. 1981. Stock assessment and life history of a newly discovered Alaska surf clam (*Spisula polynyma*) resource in the southeastern Bering Sea. Can. J. Fish. Aquat. Sci. 38: 1173 – 1181.

Lors d'un relevé d'exploration des ressources subtidales de coques en 1977 dans le sud-est de la mer de Béring, on a découvert de fortes concentrations de palourdes de

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Stimpson, *Spisula polynyma*, le long de la côte nord de la péninsule d'Alaska. Par la suite, des croisières d'évaluation de stock en 1977 et 1978 avec l'appareil de récolte hydraulique en usage sur la côte est ont permis de définir un stock géographiquement isolé d'une biomasse exploitable estimée à 329 000 ± 52 000 t et un rendement potentiel annuel calculé, de façon conservatrice, à 25 017 t (rendement maximum soutenu) de palourdes entières. Des essais de rendement par pêche à 13 sites en 1978 donnèrent des prises par unité d'effort de 815 kg/h avec un récolteur hydraulique de 1,84 m de large.

Des études du cycle biologique indiquent que l'espèce a une longue durée de vie (25 ans), croît lentement ($K = 0{,}135$), est pleinement recrutée à la population reproductrice à l'âge de 8 ans, est sujette à une faible mortalité naturelle calculée de façon conservatrice à ($M = 0{,}19$) et atteint une biomasse maximale de cohorte aux âges compris entre 9,4 et 13,0 ans. Nous présentons les fondement biologique des mesures de gestion.

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BROAD-RANGE studies, jointly funded by U.S. Federal and State of Alaska agencies together with eight private companies, were conducted in 1977–78 to investigate the potential for establishing a fishery for the Alaska surf or pink neck clam (*Spisula polynyma*) in the subtidal waters of the southeastern Bering Sea.

Exploratory surveys resulted in the discovery of a *S. polynyma* resource distributed over a 6800 km^2 area of the continental shelf near the north coast of the Alaska Peninsula. Reports have been completed describing fishing gear, general resource distribution, harvesting feasibility, preliminary estimates of abundance, and meat quality (Hughes et al. 1978; Hughes and Nelson 1979). An additional goal of the surveys and subject of this study was the life history of *S. polynyma* and detailed resource assessment data for management purposes. Results represent the first in-depth study of the species from its predominantly subtidal habitat although it is known to have a circumpolar distribution and occurs near the heavily harvested Atlantic surf clam *S. solidissima* resources in the north Atlantic.

Establishment of a fishery for the Alaska surf clam resource seems likely; consequently, it is desirable (and somewhat unusual) to have baseline biological data available for managing the resource prior to its commercial harvest.

Materials and Methods

Field operations were conducted from the 29-m fishing vessel *Smaragd* (750 hp; 1 hp = 746 W) in 1977 and the 30-m fishing vessel *Sea Hawk* (650 hp) in 1978. Survey gear in 1977 consisted of a 6000-kg east coast, hydraulic jet clam harvester with 0.9-m (3-ft) knife (fishing width). The 1978 harvester was lighter (3000 kg) and equipped with a 1.8-m (6-ft) knife. Water was supplied to the harvester's jet manifold through a 15-cm (6-in.) diameter hose from a 11 350 L/min pump (1977) and 15 135 L/min pump (1978) driven by a 350-hp, deck-mounted diesel engine. The harvesters were set and retrieved by trawal winches and towed behind the vessel with 7.5-cm (3-in.) diameter polypropylene line (Hughes et al. 1978; Hughes and Nelson 1979).

SURVEY DESIGN

Three types of survey operations were conducted: exploratory fishing, resource assessment, and production fishing. Initial exploratory fishing, and the first resource assessment survey were completed during a 32-d period in July–August 1977. The second resource assessment survey and production fishing studies were completed during a 38-d period in July–August 1978.

The exploratory fishing survey was designed to locate general areas of clam concentration and covered a wide geographic area at low sampling density. Accordingly, 106 tows of 15–30 min duration were completed over a 20 000 km^2 area of the southeastern Bering Sea (Fig. 1, blocks 1–66). Resource assessment surveys in 1977 and 1978 were designed to determine geographic and bathymetric distribution and abundance of *S. polynyma* in areas where concentrations were detected during the exploratory survey. A total of 365 tows of 10–15 min duration at random sites were completed along the north coast of the Alaska Peninsula in survey blocks 40–66 (Fig. 1) which collectively comprise an area of 6800 km^2. Thirteen areas of high clam density encountered during the assessment surveys were fished intensively to determine commercial production catch rates. During this operation, 254 tows of 10–30 min duration were completed.

CATCH SAMPLING

Standard deck sampling procedures (Hughes 1976) were employed to determine species catch composition, catch rates, size composition, age composition, and maturity. Shell length frequency measurements (nearest millimetre) were randomly collected from each 1977 resource assessment tow and at each 1978 production fishing site with desired sample size being 300 clams. Two 1977 and two 1978 independent stratified samples of *S. polynyma* shells (25 clams/5-mm length interval) were collected for age analysis and one 1977 stratified sample of whole animals (10 clams/5-mm length interval) was collected to determine the shell length–round weight relationship.

Gonads for stage of development studies collected in 1977–78 (5 clams/5-mm length interval) were cross-sectioned and fixed in the field with modified Davidson's fixative (Formalin–95% ethanol–glacial acetic acid–distilled water; 2:1:3). Upon arrival at the laboratory gonads were washed in 50% ethanol, dehydrated, blocked in paraffin, sectioned at 6–10 μm, and stained with Harris modified hematoxylin and eosin (H + E).

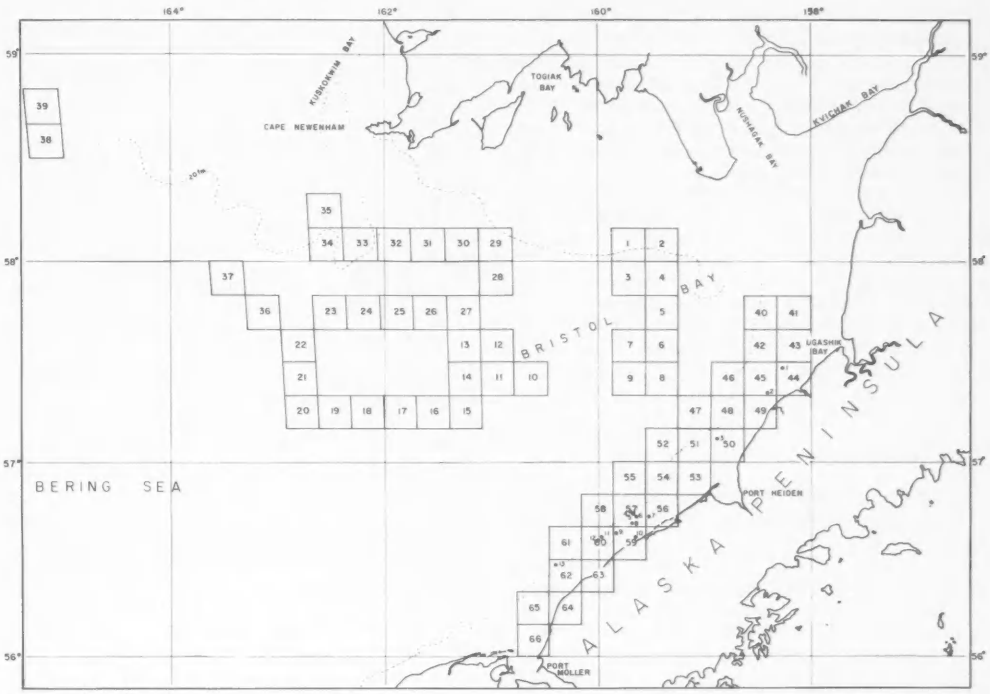

FIG. 1. Location of numbered survey blocks in the southeastern Bering Sea where surveys of the Alaska surf clam (*S. polynyma*) were completed. Initial explorations were conducted in each block; the 1977 and 1978 resource assessment surveys were conducted within blocks 40–66 along the north coast of the Alaska Peninsula and production fishing studies in 1978 were undertaken at the 13 dotted locations within survey blocks. Each survey block represents 343 km^2 or 100 nautical square (10 miles × 10 miles) miles.

DATA ANALYSIS

Shell length frequency distributions determined from the 1977 resource assessment survey were weighted by catch magnitude and area within survey blocks, whereas length data collected during the 1978 production fishing studies were weighted only by catch magnitudes.

Growth was determined by measuring shell length at each annulus after the method described by Weymouth et al. (1925), discussed by Wilbur and Owens (1964) and used by various workers to measure age and growth in bivalves. Measurements were made with calipers to the nearest millimetre; length was the straight line distance between the anterior and posterior margins of an annulus. Use of this method to determine age and growth depends on whether annuli are formed and whether they can be distinguished on the surface of the shell. Suf clams from the Bering Sea have distinct annuli; those animals with indistinct annuli (less than 5% of the sample) were discarded. Annuli up to about age 14 were distinct and easily read but beyond age 14 they tended to be more obscure. Measurements of *S. polynyma* past this age cannot be considered as precise as those of younger clams and animals beyond 19 yr were not included in growth and mortality studies due to increased aging difficulties.

Mean observed (total) shell length at age data obtained from the two 1977 and two 1978 stratified shell samples were compared for within-year variation and subsequently combined into one 1977 and one 1978 age–length key because differences were insignificant. Resulting proportions of observed ages at each length were applied to respective 1977 and 1978 weighted length frequencies. For this we used a computer program by Allen (1966) modified to exclude extrapolations beyond the age–length range and to include the calculation of mean length at age as well as numbers at age. This analysis provided weighted age composition data and mean length at age data for growth studies.

Von Bertalanffy growth in length parameters were determined from the above-observed age–length data and separately from 1977 and 1978 age–length data obtained from back-measured age rings. Although each technique has been used in past studies, they do not appear to have been compared from a given sample. Thus we considered it of scientific interest to compare growth parameters resulting from the observed and back-measured age–length data sets.

An area swept technique (Alverson and Pereyra 1969) was employed to estimate exploitable biomass using the relation

$$\bar{P}w = \frac{(\text{CPUE})(A)}{c \quad a}$$

where $\bar{P}w$ is equal to the average standing stock in weight of the catchable population, CPUE is catch per standard unit of effort, A is the total area, a is the bottom area covered by the clam harvester, and c is a coefficient related to the effectiveness of the harvester in capturing *S. polynyma*. In this study, c was assumed to equal 1 (100% efficient). Although c is undoubtedly less than 1, the true value is unknown; hence biomass estimates are probably conservative.

Stock yield was obtained from the relationship MSY = 0.4 $M\bar{P}w$, where MSY is the maximum sustained yield, M is the instantaneous mortality coefficient, and $\bar{P}w$ is the estimated exploitable biomass (Alverson and Pereyra 1969). The relationship MSY = 0.4 $M\bar{P}w$ was used rather than the MSY = 0.5 $M\bar{P}w$ of Gulland to provide a more conservative estimate of biomass as outlined by Alverson and Pereyra.

All data are stored at the computer facility, Northwest and Alaska Fisheries Center, NMFS, Seattle, Washington.

Results

Stock Description

The initial exploratory survey indicated extremely low or no *S. polynyma* concentrations in the offshore southeastern Bering Sea, blocks 1–39 (Fig. 1) but a potential resource along the north coast of the Alaska Peninsula between Port Moller and Ugashik Bay. Ensuing resource assessment surveys in 1977 and 1978 delineated a *S. polynyma* resource throughout survey blocks 40–65, a 6800 km^2 area.

Concentrations were not located southwest of Port Moller, perhaps due to the increasing occurrence of hard and rocky substrates noted in this area. The lack of *S. polynyma* concentrations northwest of Ugashik Bay may be related to freshwater influence from the Bristol Bay area. Optimal salinities northeast of Ugashik Bay average 29‰ or less compared with 32‰ common to the remainder of the Alaska Peninsula including that area in survey blocks 40–65 (Ingraham 1981). Within the resource area, *S. polynyma* was found to be most dense at depths of 30–32 m (Fig. 2). It appears the resource represents an isolated stock unit due perhaps to unfavorably low salinities at the northern extremes, unfavorably hard substrates at the southern extremes, excessive depths in a western direction, and the land mass of the Alaska Peninsula to the east. Furthermore, a free genetic exchange within that area seems apparent from the massive spawning activity which occurred throughout the stock's geographic distribution during July–early August 1977 and 1978.

Size, Age, and Sexual Maturity

Data depicting size, age, and maturity composition of the stock were obtained during the initial resource assessment survey in 1977. That assessment was conducted within a 5440 km^2 area representing 70% of the 6800 km^2 area occupied by the stock. Shell length size compositions of 10 318 animals measured during that survey were weighted by catch magnitude and area within sampling blocks to determine a weighted size composition of the stock (Fig. 3). Weighted age composition (Fig. 4) was determined from the 1977 age–length key and the weighted shell length composition presented above.

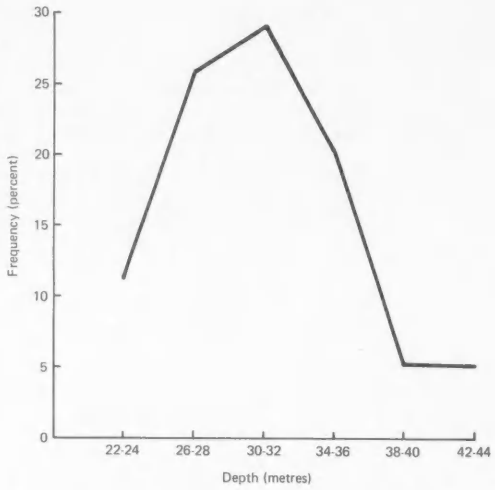

FIG. 2. Depth-dependent density distribution of the *S. polynyma* stock off the north coast of the Alaska Peninsula as determined during the 1977 resource assessment survey using a 0.92-m (3-ft) wide hydraulic clam harvester.

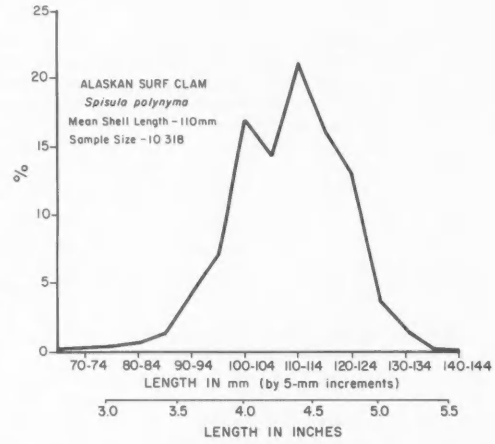

FIG. 3. Weighted shell length size composition of the *S. polynyma* stock off the north coast of the Alaska Peninsula, 1977.

All *S. polynyma* examined were dioecious. Males and females collected in July and August 1977 and 1978 were ripe, spawning, or recently spent. Male and female animals as young as 5 yr of age (mean shell length of 63 mm) were found sexually active but represented only 10% of that age-group. All 8-yr-old clams (mean shell length 83 mm) were sexually active and represented the youngest age-group fully recruited to the spawning population.

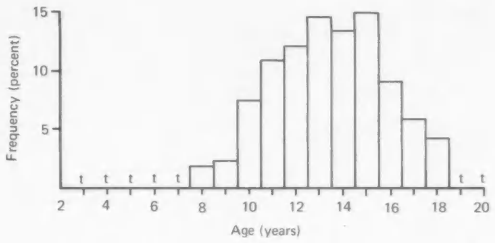

FIG. 4. Weighted age composition of the *S. polynyma* stock off the north coast of the Alaska Peninsula, 1977. (t = trace.)

LENGTH–WEIGHT RELATIONSHIP AND MEAT YIELD

Length–weight data for males and females combined was determined from 184 animals collected during the 1977 resource assessment survey. The length–weight relationship of 30- to 146-mm clams, determined by fitting the logarithmic form of the equation $W = gLd$ when W is whole body weight in grams and L is shell length in millimetres, is shown in Fig. 5.

Yield of edible meat was determined by hand shucking 100 kg of fresh *S. polynyma* and weighing the meat and liquid

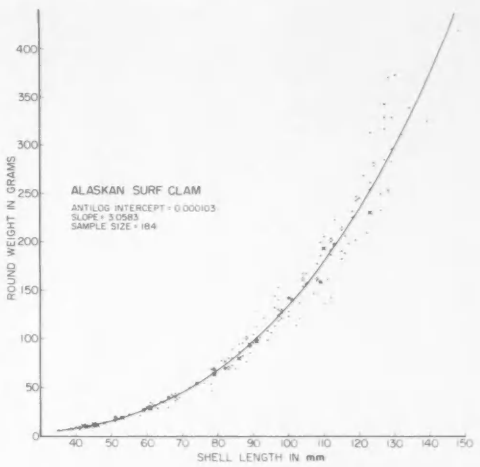

FIG. 5. Shell length–round weight relationship of *S. polynyma* off the north coast of the Alaska Peninsula, 1977.

TABLE. 1. Calculated *Spisula polynyma* exploitable biomass (tonnes) from the north coast of the Alaska Peninsula by survey block from the 1977, 1978, and 1977–78 combined resource assessment surveys.

		1977		1978		1977–78 data combined	
Block No.	Area (km^2)	No. of tows	Biomass estimate (tonnes)	No. of tows	Biomass estimate (tonnes)	No. of tows	Biomass estimate (tonnes)
40	343	1	2 703	0	—	1	2 703
42	343	2	1 757	5	19 705	7	14 493
43	343	0	—	10	22 132	10	22 132
44	206	0	—	14	15 208	14	15 028
45	343	22	58 279	21	31 993	43	40 476
46	343	3	6 249	0	—	3	6 249
48	343	9	11 037	4	3 878	13	7 562
49	240	4	8 792	6	6 099	10	6 595
50	333	10	53 530	31	32 996	41	35 867
51	343	2	27	5	18 563	7	13 266
54	343	2	1 409	0	—	2	1 409
55	343	1	378	0	—	1	378
56	240	0	N.D.	17	15 276	17	15 276
57	343	15	18 361	47	57 857	61	48 091
58	343(69)[a]	1	23 114[a]	0	—	1	4 623[a]
59	185	7	16 026	22	30 508	29	26 368
60	329	21	31 194	38	44 429	59	37 879
61	343(69)[a]	12	33 255[a]	0	0	12	5 543[a]
62	295	18	19 803	14	35 856	32	24 971
65	343	2	270	0	—	2	270
Totals	6 990	132	286 184	234	334 320	365	329 179
Biomass range at 95% confidence level			248 294–324 074		302 574–376 093		277 172–381 186

[a]The fishable area in blocks 58 and 61 was overestimated in the 1977 survey. Soundings in these blocks in 1978 indicated each block contained only about 69 km^2 of fishable seabed. Combined 1977–78 biomass figures reflect this change.

TABLE. 2. Catch rates and mean shell length size composition of *Spisula polynyma* at 13 production fishing sites along the north coast of the Alaska Peninsula, 1978. Fishing was conducted with a 1.84-m (6-ft) wide hydraulic clam harvester equipped with a 5-cm (2-in.) diameter ring collecting bag.

Production site No.	Survey block No.	Fishing effort (h)	Total catch (kg)	Catch per hour		Mean shell length
				(kg)	(bushels)	(mm)
1	44	1.67	686	411	11.3	124
2	45	1.40	855	611	16.8	124
3	50	2.47	1 667	675	18.6	107
4	57	11.08	8 100	731	20.1	103
5	57	2.60	2 326	894	24.6	111
6	57	9.15	7 327	801	22.0	119
7	56	1.83	1 592	870	23.9	112
8	57	1.67	2 154	1 290	35.5	117
9	59	1.50	1 379	919	25.3	123
10	59	13.05	8 289	635	17.5	112
11	60	1.02	725	711	19.6	120
12	60	2.53	2 297	907	25.0	123
13	62	2.17	2 485	1 147	31.5	108
All sites		52.14	39 882	Mean 815	22.2	Mean 113

fractions. Total whole meats and liquid weighed 55 kg, drained whole meats 37 kg, and drained eviscerated meats 29 kg. The above meat yields were obtained in July when clams were in spawning condition. Meat yields at other times of the year have not been determined.

ESTIMATES OF STANDING STOCK

Exploitable biomass estimates were calculated by survey block for the 1977, 1978, and 1977–78 combined resource assessment surveys (Table 1). Although most survey blocks were assessed each year, work was not completed in blocks 44, 46, and 56 during 1977 nor in blocks 40, 46, 54, 55, 58, and 61 in 1978. Thus the 1977–78 combined surveys provided coverage of all blocks occupied by the resource, 40–65, but total biomass estimates for 1977 and 1978 are not directly comparable due to these differences in geographic coverage. We believe the combined 1977–78 survey data provide the most accurate baseline estimate of the described *S. polynyma* exploitable stock, 329 179 ± 52 000 t of whole clams (95% confidence level).

PRODUCTION TESTS

Production fishing tests were completed in 1978 at 13 sites along the north coast of the Alaska Peninsula (Fig. 1) to assist industry and management's evaluation of potential for a future commercial fishery. Table 2 summarizes catch–effort data and mean shell length of *S. polynyma* obtained at each production site. Weighted size and age composition of combined production site catches shown in Fig. 6 represent the distribution of size and age expected from commercial harvest of the resource.

GROWTH

Length–age data from the 1977 and 1978 surveys were fitted by the Von Bertalanffy relation $l_t = L\alpha(1 - e^{-kt-t_0})$ following computational procedures by Fabens (1965).

Growth patterns and parameters were determined from means of the observed lengths at age obtained from the composite year-classes represented, and separately from mean lengths at age determined from back-measured growth rings. Two estimates of growth were then derived from these data. Although the back-measured growth data were not separated into age-classes, they nonetheless provide the best estimate of growth parameters. Total length at age data are likely to indicate an unrealistic growth pattern because of biased sampling, i.e. the gear would select the largest of younger clams. Although the same problem exists potentially in the clams used for back measurement, the bias is mediated by inclusion of clams of all ages in calculating the mean length at annulus.

Sets of observed mean lengths for ages 3–19 yr and back-measured mean lengths for ages 0.5–18.5 yr are summarized by survey year in Table 3 with respective sets of growth parameters. (Age increments by the fraction of a year between middates of spawning (July) and age ring formation (January–February) were assigned to data from back-measured age rings while no adjustment was assigned to the observed length at age data due to a July sampling date.) Accompanying growth curves showing departures from fit are presented for the 1977 and 1978 observed (Fig. 7) and back-measured (Fig. 8) data. As mentioned above, the back-measured growth data provided the best estimate of growth parameters and indicated a mean growth completion rate (K) of 0.135.

MORTALITY AND STOCK YIELD

An important management aspect of this study was to determine initial estimates of stock yield from biomass which requires knowledge of the mortality rate. Baseline instantaneous mortality coefficients of the virgin *S. polynyma* stock ($M = Z$) were calculated realizing that annual recruitment strength is variable and that mortality rate generally increases with age. Consistent with the biomass calculations where the average of survey data for 2 yr constituted the best abundance base line, we believe the 2 yr of observed age composition

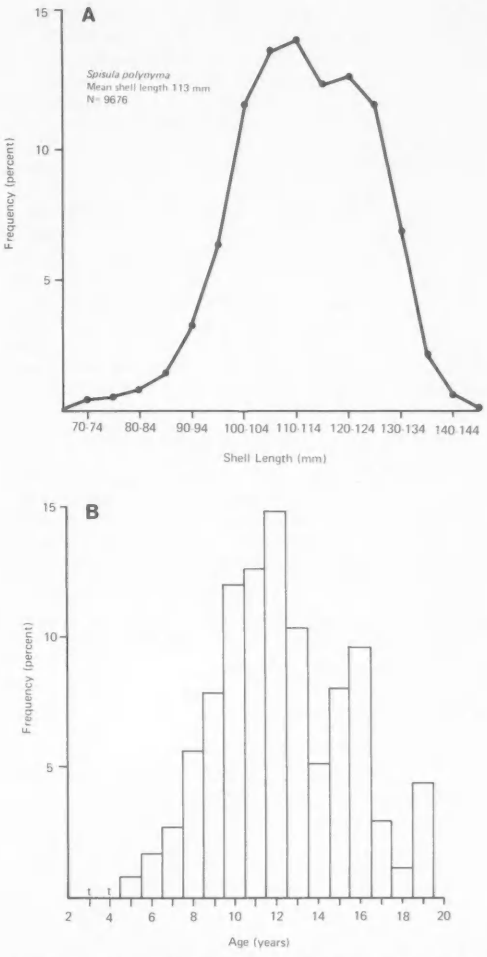

FIG. 6. Weighted shell length size (A) and weighted age (B) composition of *S. polynyma* catches at 13 production fishing sites along the north coast of the Alaska Peninsula, 1978. Data represent the projected size and age composition of landings using a hydraulic clam harvester equipped with a 5-cm (2 in.) ring diameter collecting bag.

TABLE. 3. Mean shell length (mm) at age and growth parameters ($L\alpha$, k, t_o) with standard deviations (σ) of departure from fit of *S. polynyma* from the north coast of the Alaska Peninsula; 1977–78 "observed" are based upon mean length at age when collected and "back-measured" are based upon age ring back measurements.

Age (yr)	Observed		Age (yr)	Back-measured	
	1977	1978		1977	1978
1	—	—	0.5	8.61	7.95
2	—	—	1.5	20.03	19.50
3	48.36	42.33	2.5	33.57	32.99
4	51.60	59.28	3.5	45.71	45.90
5	63.18	63.05	4.5	57.47	57.62
6	75.24	74.21	5.5	67.40	67.77
7	89.30	81.89	6.5	75.82	76.49
8	89.64	91.52	7.5	82.95	83.83
9	91.24	92.74	8.5	88.97	89.72
10	97.64	96.72	9.5	94.36	95.03
11	100.80	101.62	10.5	98.96	100.09
12	104.19	105.37	11.5	103.17	104.43
13	109.32	109.50	12.5	106.89	108.22
14	111.46	115.80	13.5	109.94	111.59
15	115.14	116.73	14.5	112.86	114.12
16	115.59	116.34	15.5	115.37	116.25
17	118.51	120.87	16.5	117.62	119.78
18	123.03	125.89	17.5	120.72	122.22
19	128.65	123.38	18.5	122.45	123.00
$L\alpha$	148.0	129.2		133.8	133.7
k	0.10	0.16		0.13	0.14
t_o	−0.94	+0.55		+0.35	+0.46
σ	3.67	2.76		0.64	0.56

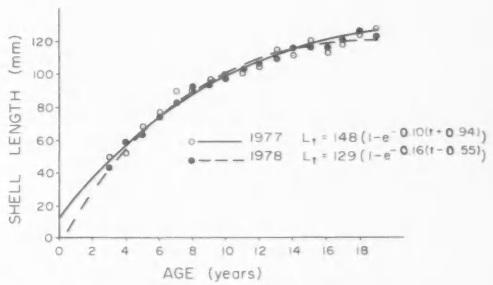

FIG. 7. Observed mean length at age with fitted growth curves of Alaska surf clam (*S. polynyma*) stock taken off the north coast of the Alaska Peninsula, 1977–78.

data constitute the best data base to calculate a baseline mortality rate. Accordingly the instantaneous total mortality rate was computed by the method of Ricker (1975) using sample frequencies of year-classes encountered at age 11 and older in 1977 and again at 12 and older in 1978, giving equal weight to each year's sample.

The resulting analysis (Table 4) indicates a baseline $M = 0.19$ ($P < 0.01$) for ages 11 and older, corresponding to sizes of 101 mm and larger.

Using the 1977–78 exploitable biomass estimate of $Pw = 329\,179$ t (Table 2) and $M = 0.19$, MSY = 25 017 t of whole clams; maximum sustained yield may also be expressed as 9256 t of drained whole meats or 7255 t of drained eviscerated meats based on our reported meat yield measurements.

Summary and Conclusion

A geographically isolated, discrete stock of Alaska surf clams (*S. polynyma*) has been described with a conservatively estimated exploitable biomass of 329 170 ± 52 000 t and potential annual yield equals 25 017 t (MSY) of whole clams.

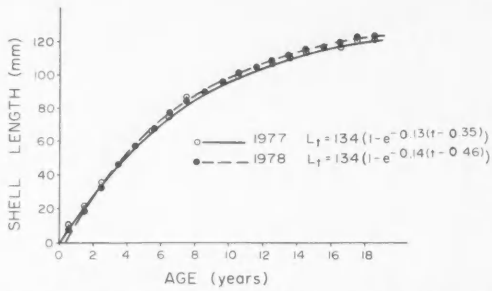

FIG. 8. Back-measured mean length at age with fitted growth curves of Alaska surf clam (*S. polynyma*) stock taken off the north coast of the Alaska Peninsula, 1977–78.

The species is long-lived (maximum observed age 25), slow growing ($K = 0.135$), is fully recruited to the spawning population at 8 yr of age, has a low natural mortality rate ($M = 0.19$), and attains maximum cohort biomass at between 9.4 and 13.0 yr of age.

The *S. polynyma* stock discovered and described as a result of this study remains unexploitable to date. Although reported stock abundance and biological parameters provide baseline knowledge, the effect of significant harvest on the resource will remain unknown until the fishery develops and changes in stock conditions are monitored. The mortality studies reported here are particularly important to future management as that parameter is the key to yield calculations. We believe the mortality rate, $M = 0.19$, is reasonable in view of the growth completion rate, $K = 0.135$, and these parameters are similar to the $M = 0.20$ and $K = 0.155$ values reported from an unexploited population of Atlantic surf clams in the Gulf of St. Lawrence (Caddy and Billard 1976).

The 1977 size composition data and mean length at age data suggest that 11-yr-old clams are the youngest age-group fully recruited to harvest gear equipped with 7.6-cm (3-in.) diameter rings in the collecting bag, and 90% of catches obtained with this gear consisted of 11- to 19-yr-old clams. The use of 5.0-cm (2-in.) diameter rings in the collecting bag lowers the age at full recruitment to the gear to 10-yr-old clams and 85% of those catches consisted of 10- to 19-yr-old clams.

Due to the sizable potential yield of the stock and production catch rates which averaged 736 kg (21.0 bushels) of clams per hour with a 1.8-m (6-ft) wide harvester, development of a clam fishery off the north coast of the Alaska Peninsula is likely in the near future. Development may be enhanced because of recent and substantial reductions in the Atlantic surf clam (*S. solidissima*) fishery.

Results of life history studies coupled with recent declines of Atlantic surf clam stocks indicated that conservative harvest levels should be maintained on the described Alaska stock for 3–5 yr to monitor changes in biological parameters resulting from fishery pressures. However, because mortality rates increase rapidly in year-classes beyond 14 yr of age, and maximum biomass production per recruit occurs at 9.4–13.0 yr of age, harvesters should be equipped with 5.0-cm (2-in.)

TABLE. 4. Age frequency of *Spisula polynyma* with estimated rates of natural mortality (M).

	1977 Sample		1978 Sample		
Year-class	N[a]	Percent year-class 1959–66	N[a]	Percent year-class 1959–66	Geometric[b] mean percent
1975	0		3		
1974	6		18		
1973	3		80		
1972	33		176		
1971	20		278		
1970	55		559		
1969	159		784		
1968	197		1 203		
1967	680		1 267		
1966	985	12.6	1 489	26.3	18.2
1965	1 098	14.1	1 036	18.3	16.1
1964	1 337	17.1	515	9.1	12.5
1963	1 209	15.5	795	14.1	14.8
1962	1 375	17.6	969	17.1	17.4
1961	818	10.5	290	5.1	7.3
1960	567	7.3	110	2.0	3.8
1959	418	5.3	448	7.9	6.5
1958	112				
Total	9 072	100.0	10 020	99.9	
Regression of ln (%) × age					
	r^2	0.5268		0.5473	0.6606
	m	0.1272		0.2504	0.1888

[a]Year-classes 1958 and 1967–75 not included in analysis.
[b]Square root $\%A \times \%B$.

diameter ring bags. This practise would target the fishery on year-classes prior to increased natural mortality, and increase the stock biomass per recruit while allowing at least two seasons of full spawning activity prior to being significantly subjected to the fishery.

A major deficiency of the reported study is the lack of knowledge regarding recruitment rates. Estimates of MSY assume constant recruitment and it appears that annual recruitment in the *S. polynyma* stock is variable. Long-term studies to determine recruitment rates and their variability would be a major asset to managers in determining more precise and long-range MSY estimates.

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ALLEN, K. R. 1966. Determinations of age distribution from age-length keys and length distributions, IBM 7090, 7094, Fortran IV. Am. Fish. Soc. 95: 230–231.

ALVERSON, D. L., AND M. J. CARNEY. 1975. A graphic review of growth and decay of population cohorts. J. Cons. Cons. Int. Explor. Mer 36: 133–143.

ALVERSON, D. L., AND W. T. PEREYRA. 1969. Demersal fish explorations in the northeastern Pacific Ocean — an evaluation of exploratory fishing methods and analytical approaches to stock assessment and yield forecasts. J. Fish. Res. Board Can. 26: 1985–2001.

CADDY, J. F., AND A. R. BILLARD. 1976. A first estimate of production from an unexploited population of the bar clam, *Spisula solidissima*. Fish. Mar. Serv. Res. Dev. Tech. Rep. 648. 13 p.

FABENS, A. J. 1965. Properties and fitting of the Von Bertalanffy growth curve. Growth 29: 265–289.

HIRSCHHORN, G. 1974. The effect of different age ranges on estimated Bertalanffy growth parameters in three fishes and one mollusk of the north-eastern Pacific Ocean, p. 192–199. *In* T. B. Bagenal [ed.] The aging of fish. Irwin Bros., Ltd., The Gresham Press, Old Woking, Surrey, England.

HUGHES, S. E. 1976. System for sampling large trawl catches of research vessels. J. Fish. Res. Board Can. 33: 833–839.

HUGHES, S. E., AND R. W. NELSON. 1979. Trial catches confirm feasibility of Bering Sea clam fishery. Natl. Fisherman Yearb. Issue 59: 36–39.

HUGHES, S. E., R. W. NELSON, AND R. NELSON. 1978. Alaskan resource may fill east coast "clam gap." Natl. Fisherman Yearb. Issue 58: 160–163.

INGRAHAM, J. W. 1981. Shelf environment. *In* D. W. Hood and J. A. Calder [ed.] Eastern Bering Sea shelf: oceanography and resources. Univ. Alaska, Fairbanks. (In press)

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish population. Fish. Res. Board Can. Bull. 191. 382 p.

WEYMOUTH, F. W., H. C. MCMILLIN, AND H. B. HOLMES. 1925. Growth and age at maturity of the Pacific razor clam, *Siliqua patula* Dixon. Bull. U.S. Bur. Fish. 41: 201–236.

WILBUR, K. W., AND G. OWENS. 1964. Growth, p. 211–242. *In* K. W. Wilbur and C. M. Yonge [ed.] Physiology of mollusca. I. Academic Press, New York and London.

Hemoglobin Levels and Red Cell Ionic Composition in Goldfish (*Carassius auratus*) Exposed to Constant and Diurnally Cycling Temperatures

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KOSS, T. F., AND A. H. HOUSTON. 1981. Hemoglobin levels and red cell ionic composition in goldfish (*Carassius auratus*) exposed to constant and diurnally cycling temperature conditions. Can. J. Fish. Aquat. Sci. 38: 1182–1188.

Hematological response in goldfish (*Carassius auratus*) held at constant temperature (20, 25, 30°C) was compared with that of animals exposed to a diurnal temperature cycle (25 ± 5°C), with particular reference to overall oxygen carrying capacity and cellular electrolytes influencing hemoglobin–oxygen affinity. All groups were sampled at 03:00, 09:00, 15:00, and 21:00. Hemoglobin and hematocrit were determined, as were plasma and packed red cell levels of water, sodium, potassium, magnesium, calcium, and chloride. The latter were used to estimate mean cellular ion concentrations. Temperature treatment influenced response. Under constant temperature conditions hemoglobin levels tended to increase at higher temperatures. This was associated with compositional changes which would be expected to reduce affinity and facilitate oxygen release. By contrast, under cycling temperature conditions hemoglobin levels were elevated whereas erythrocytic electrolyte concentrations tended to be stable. Observations are discussed in terms of their bearing on the interpretation of studies on the acclimatory process.

Key words: goldfish, *Carassius auratus*; blood chemistry, temperature, hemoglobin, O_2-carrying capacity

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On trouvera dans l'article qui suit les résultats d'une comparaison de la réponse hématologique de carassins (*Carassius auratus*) maintenus à température constante (20, 25, 30°C) avec celle d'animaux d'exposés à un cycle nycthéméral de températures (25 ± 5°C), en particulier sous le rapport de la capacité générale de charge d'oxygène et des électrolytes cellulaires qui influent sur l'affinité hémoglobine–oxygène. Tous les groupes ont été échantillonnés à 03:00, 09:00, 15:00 et 21:00. L'hémoglobine et l'hématocrite ont été déterminées, ainsi que les niveaux, dans le plasma et les globules rouges concentrés, d'eau, sodium, potassium, magnésium, calcium et chlorure. Ce dernier a servi à estimer les concentrations cellulaires moyennes d'ions. La température influe sur la réponse. Dans des conditions de température constante, les niveaux d'hémoglobine tendent à augmenter aux températures élevées. Ceci est associé à des changements dans la composition qui, on peut s'y attendre, réduisent l'affinité et facilitent la mise en liberté de l'oxygène. Par contre, dans des conditions cycliques de température, les niveaux d'hémoglobine s'élèvent tandis que les concentrations d'électrolytes érythrocytiques tendent à demeurer stables. Nous analysons ces observations en fonction de l'influence qu'elles peuvent avoir sur l'interprétation d'études sur les processus d'acclimatation.

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GOLDFISH (*Carassius auratus*) can tolerate temperatures ranging from ~0 to 40°C (Fry et al. 1942). Between these extremes standard oxygen consumption rises by at least one order of magnitude while oxygen availability decreases by 50% or more (Beamish and Mookherjii 1964). Several responses to this type of respiratory stress have now been observed at the hematological level (Houston 1980). Modest increases in hemoglobin content and red cell numbers usually accompany acclimation to higher temperature and are often associated with some reduction in mean erythrocytic volume. Species having multiple hemoglobin systems typically alter the concentrations of specific hemoglobins. Cellular levels of factors (e.g. Cl^-, P_i^{2-}, Mg^{2+}, ATP, GTP) known to influence hemoglobin–oxygen affinity are modified and, to some extent at least, these changes can be correlated with modifications in oxygen loading and release tensions.

In common with most studies upon the nature and con-

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sequences of the acclimatory process, however, virtually all those concerned with its hematological manifestations have been based on long-term exposure of test animals to precisely controlled temperatures. Implicit to such investigations is the assumption that temperature level per se is the critical variable. However, for many species such circumstances are unusual, if not abnormal. The relatively shallow, slow-flowing waters in which goldfish are locally abundant commonly undergo substantial daily temperature fluctuations during the summer months, often under circumstances which preclude resorting to avoidance behaviors. For these animals direction and rate of temperature change, as well as the ambient temperature level, may operate in control of acclimatory response.

The present study was undertaken to compare hematological responses to constant temperature conditions with those which develop under the more ecologically realistic circumstances provided by a daily temperature cycle. An earlier study revealed significant alterations in hemoglobin types and concentrations under such conditions (Houston and Rupert 1976). In this investigation emphasis has been given to the cellular ionic environment in which these hemoglobins function.

Materials and Methods

Goldfish of both sexes (mean weight ± 1 SE, 32.6 ± 1.11 g) were obtained from local suppliers and held in 200-L recirculating Fibreglas tanks equipped with laterally positioned air bars and high-capacity (~5 $L \cdot min^{-1}$) suction filters. The dechlorinated and aged St. Catharines city water used was of moderate total hardness (~140 $mg \cdot L^{-1}$, as $CaCO_3$) and alkalinity (~95 $mg \cdot L^{-1}$, as $CaCO_3$) and ranged in pH from 7.2 to 7.6. Oxygen content varied inversely with temperature, but exceeded 80% saturation. Each tank was provided with a photoperiod hood, and all groups were held on a 12-h light:12-h dark photoperiod schedule in which light periods began at 07:00.

Constant temperature acclimation tanks were controlled to within ±0.15°C of set point. A low-frequency sinewave generator was used to drive a 24-h temperature cycle. This was accurate to approximately ±4 $min \cdot d^{-1}$ and consistent to within 0.5°C on successive cycles. The cycle was designed to mimic local conditions without exposing the fish to acute thermal stress. Thermal tolerance, scope-for-activity, and growth rate data indicate that the optimum temperature of the goldfish is close to 25°C. This was chosen as the cycle midpoint. The sinewave form adopted provided equal periods of exposure to temperatures above and below the midpoint. Cycle peak (30°C) and minimum (20°C) temperatures corresponded to summer variations in regional waters where goldfish are abundant.

Following transfer to acclimation tanks animals were held at 22–24°C for 10 d. Temperatures were then adjusted by about $1°C \cdot d^{-1}$ until the desired constant temperatures (20, 25, 30°C) were established. Animals to be exposed to cycling temperatures were first brought to the midrange temperature (25°C). Cycle amplitude was then increased by approximately $\pm 1°C \cdot d^{-1}$ to 25 ± 5°C. All animals were held for at least 3 wk before sampling. There were no deaths during acclimation and all fish appeared to be healthy.

Fish exposed to the cycle were sampled at 03:00 (20°C), 09:00 (25°C), 15:00 (30°C), and 21:00 (25°C). Sampling at 03:00 and 21:00 was carried out under dim red light to minimize disturbance. Fish at constant temperature were simultaneously sampled to provide appropriate controls, i.e. 20°C at 03:00, 25°C at 09:00 and 21:00, and 30°C at 15:00. In addition, because there is little information available on diurnal variation in blood oxygen carrying capacity, and none relating to red cell ionic composition, sampling of these animals was expanded to include all intervals. The acclimation and sampling program was repeated three times and all data were pooled to give samples of 15–25 specimens at each temperature and sampling period.

Blood samples were drawn from caudal vessels into oiled, ammonium heparin-treated syringes and chilled. Hematocrit and hemoglobin were immediately determined, the latter by the alkaline hematin technique (Anthony 1961). The remainder of each sample was centrifuged (5000*g*, 5 min, 20–23°C) and plasma drawn off by micropipette. Plasma remaining in contact with the packed cell column was removed by absorption to filter paper. All samples were stored in individual sealed plastic containers at −76°C. Earlier studies have shown that under these conditions there are no significant changes in water or ion content for at least 1 yr (Houston and Smeda 1979).

A Perkin–Elmer model 372 atomic absorption spectrophotometer was used in the emission mode for sodium and potassium determinations and in the absorption mode for magnesium and calcium. Chloride determinations were conducted with the Buchler–Cotlove chloridometer.

Determinations carried out on packed cell samples were corrected for plasma retained in the interstices of the cell columns. This correction factor, 2.8% of packed cell volume, was obtained by addition of [^{14}C]PEG-4000 to carp (*Cyprinus carpio*) whole blood samples prior to centrifugation (Houston and Smeda 1979). A similar value (3%) has been reported for goldfish blood by Catlett and Millich (1976) on the basis of [^{14}C]inulin addition. Moisture content was estimated by desiccation (24 h at 70°C, followed by 48 h at 103°C) and the corrected values were used to calculate red cell electrolyte concentrations. The resulting values are means for the entire aqueous phase and do not take into account the specific or nonspecific interactions of these ions or the effects of compartmentalization.

Data evaluations were carried out by single classification analysis of variance. All values were routinely transformed to base-10 logarithms or arc-sin equivalents, as appropriate, and significance was attributed to differences at the 0.05 level or better.

Results

Response to Constant Temperature Conditions

Significant diurnal variations in hemoglobin and hematocrit were observed at all acclimation temperatures (Table 1). No consistent pattern was apparent in the sense that minimum or maximum values were associated with specific sampling periods. At times other than 21:00 some increase in hemoglobin content was apparent at higher temperatures, and this was true of hematocrit as well.

TABLE 1. Time- and temperature-related variation in the hemoglobin (g · 100 mL^{-1} whole blood) and hematocrit (% whole blood) of goldfish acclimated to 20, 25 and 30°C and sampled at 03:00, 09:00, 15:00, and 21:00.

	20%		25°C		30°C		Significance	
Time	Hemoglobin	Hematocrit	Hemoglobin	Hematocrit	Hemoglobin	Hematocrit	Hemoglobin	Hematocrit
03:00	6.5±0.34(19)[a]	23.7±1.13(19)	8.5±0.53(17)	28.5±0.95(17)	8.6±0.36(15)	28.9±1.11(15)	20 25 30	20 25 30
09:00	6.9±0.45(18)	25.9±1.39(18)	6.8±0.29(19)	25.4±0.86(19)	7.8±0.62(15)	28.5±1.15(15)	20 25 30	20 25 30
15:00	8.0±0.38(18)	28.3±1.25(18)	7.6±0.35(18)	29.7±0.74(18)	8.2±0.41(25)	27.9±1.12(25)	NS[b]	NS
21:00	7.9±0.33(18)	29.9±0.99(18)	7.3±0.31(17)	28.6±0.63(17)	7.0±0.42(15)	24.0±0.76(15)	NS	20 25 30
Significance	03 09 15 21[c]	03 09 15 21	03 09 15 21	09 03 15 21	03 09 15 21	03 09 15 21		

[a]Mean ± 1 SE (sample number).
[b]Not significantly different at the 0.05 level.
[c]Values underlined not significantly different at the 0.05 level.

Red cell water content was not significantly influenced by temperature (Table 2) and significant diurnal variation was observed only at 30°C. No ion other than chloride exhibited consistent diurnal concentration changes. Chloride, however, was lower at 03:00 than at other sampling periods. By contrast, relatively consistent though not uniformly significant changes were observed in relation to temperature. Sodium and chloride increased at higher acclimation temperatures, magnesium and calcium declined, and potassium tended to be lower at 25°C than at either 20 or 30°C.

Response to Cycling Temperature Conditions

By comparison with animals held at constant temperature and sampled at corresponding times and temperatures, hemoglobin and hematocrit in fish exposed to cycling temperatures were both high and diurnally stable (Fig. 1).

Distinct differences in red cell composition were also associated with acclimation to constant and cycling temperature conditions, the single exception to this being seen in relation to water content (Fig. 2). Cellular potassium concentrations decreased significantly with cycle progression, but under all temperature–time combinations exceeded corresponding values in fish at constant temperature. The converse was true of sodium. Calcium was diurnally stable at concentrations well below those characteristic of animals at constant temperature. Chloride and magnesium were less variable in relation to time and temperature than was the case at constant temperature. Photoperiod appeared to influence composition. Under both constant and cycling temperature conditions, specimens sampled during dark periods (03:00, 21:00) had lower water and sodium levels than did those at 09:00 and 15:00. Potassium concentrations were higher under these circumstances and this tended to be the case with magnesium as well. Calcium also followed this pattern in the constant temperature groups.

Discussion

The problem of satisfying temperature-related increases in oxygen demand is essentially one of ensuring branchial uptake, circulatory transport, and tissue level release of oxygen in amounts and at rates adequate to meet cellular requirements. At the hematological level the former is a question of oxygen carrying capacity, the latter, one of hemoglobin–oxygen affinity.

The most obvious resolution of the first lies in increasing hemoglobin levels. The goldfish, in company with other species, has proven inconsistent in this respect. Under apparently similar temperature conditions obviously adaptive responses have been reported (e.g. increases in hemoglobin, hematocrit, red cell numbers, and(or) mean erythrocytic hemoglobin content; reductions in mean erythrocytic volume) as have apparently antiadaptive changes (e.g. decreases in hemoglobin, hematocrit, and(or) red cell numbers) and the absence of significant changes (Spoor 1951; Anthony 1961; Linn 1965; Falkner and Houston 1966; Houston and Cyr 1974; Catlett and Millich 1976; Houston et al. 1976; Houston and Rupert 1976). In part, at least, these inconsistencies may stem from the fact that overall oxygen uptake is a product

TABLE. 2. Time- and temperature-related variations in red cell water content ($g \cdot kg^{-1}$ packed cells) and Na^+, K^+, Mg^{2+}, Ca^{2+}, and Cl^- concentrations ($mmol \cdot L^{-1}$ cell water) in goldfish acclimated to 20, 25, and 30°C and sampled at 03:00, 09:00, 15:00, and 21:00. Sample sizes as in Table 1.

	Time	20°C	25°C	30°C	Significance
Water	03:00	690.8±9.5[a]	689.1±8.6	701.4±8.6	NS
	09:00	687.9±15.3	694.9±7.4	681.0±8.2	NS
	15:00	696.5±12.9	695.9±6.7	704.3±4.5	NS
	21:00	703.2±9.7	683.7±10.6	694.0±11.1	NS
	Significance	NS[b]	NS	09 21 03 15[c]	
Sodium	03:00	17.6±1.44	21.5±2.05	23.6±2.93	NS
	09:00	17.9±1.17	25.3±1.25	24.0±2.00	20 25 30
	15:00	15.6±1.04	18.0±1.38	25.2±1.49	20 25 30
	21:00	15.8±1.08	19.3±1.96	23.8±1.70	20 25 30
	Significance	NS	03 09 15 21	NS	
Potassium	03:00	147.4±2.96	140.6±1.56	145.3±4.91	NS
	09:00	152.9±3.62	132.9±1.65	149.7±3.13	25 20 30
	15:00	148.8±3.55	134.3±1.62	139.3±1.70	25 20 30
	21:00	138.0±2.71	141.1±3.94	144.2±2.42	NS
	Significance	03 09 15 21	03 21 15 09	09 09 21 15	
Magnesium	03:00	11.5±0.25	11.1±0.41	9.4±0.27	20 25 30
	09:00	11.7±0.37	10.0±0.28	9.6±0.23	20 25 30
	15:00	11.9±0.54	9.9±0.28	9.5±0.22	20 25 30
	21:00	11.1±0.34	10.3±0.20	9.9±0.25	20 25 30
	Significance	NS	03 21 09 15		
Calcium	03:00	0.5±0.06	0.3±0.03	0.1±0.01	20 25 30
	09:00	0.5±0.03	0.2±0.03	0.1±0.02	20 25 30
	15:00	0.4±0.02	0.3±0.06	0.2±0.04	20 25 30
	21:00	0.4±0.01	0.3±0.05	0.2±0.03	20 25 30
	Significance	NS	NS	NS	
Chloride	03:00	97.9±2.77	100.1±4.84	107.5±1.49	20 25 30
	09:00	105.1±3.86	110.5±2.32	114.9±1.18	20 25 30
	15:00	111.5±4.13	111.2±2.28	118.8±1.48	NS
	21:00	106.2±2.96	111.4±1.84	111.5±3.44	20 30 25
	Significance	03 09 21 15	03 09 15 21	03 15 21 09	

[a]Mean ± SE (sample numbers as in Table 1).
[b]Not significantly different at the 0.05 level.
[c]Values underlined not significantly different at the 0.05 level.

function of carrying capacity and several systemic variables (Hughes 1964). Relatively small increases in hemoglobin content in conjunction with increases in ventilatory flow, cardiac output, and effective lamellar area can produce significant increases in oxygen uptake. Conversely, however, the effects of small decreases in capacity are readily masked by increases in systemic activity.

In the present investigation increases in hemoglobin concentration and hematocrit accompanied acclimation to higher temperatures. Extent of response was, however, apparently influenced by acclimation regime. A more-or-less direct but diurnally variable relationship between hemoglobin, hematocrit, and temperature characterized groups exposed to constant temperature conditions. Those under cycling conditions appeared to respond in relation to the oxygen demand associated with maximum temperature despite their relatively brief and intermittent exposures to cycle peaks.

The individual components of teleostean hemoglobin systems frequently differ in their affinities for oxygen and the extent to which these can be altered by affinity-modulating factors. Consequently, the kinds of hemoglobins present and the circumstances under which they function may be adaptively significant. Goldfish are unusual in that they have two hemoglobins at low temperature, an additional fraction at temperatures above 10−12°C, and oscillate between these conditions when exposed to a diurnal temperature cycle (Houston and Rupert 1976). Under the conditions obtained in this study all groups would be expected to have three-component systems. The ionic environment within which these hemoglobins operated did, however, vary with temperature. Furthermore, the changes seen appear to have been adaptively appropriate. Although oxygen content varied inversely with temperature, tensions remained at levels adequate for oxygen loading, i.e. increases in oxygen requirements were not associated with markedly hypoxic conditions. Under such circumstances reductions in affinity are desirable, for these would facilitate oxygen release to tissues.

Studies upon mammalian and fish hemoglobin systems have revealed a consistent pattern of ionic effects upon the oxygen affinities of hemoglobins sensitive to such factors

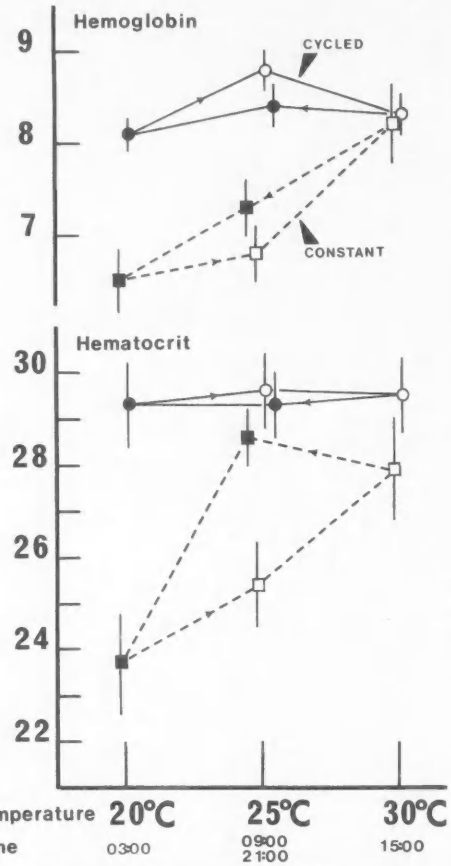

FIG. 1. Variations in hemoglobin ($g \cdot 100\ mL^{-1}$ whole blood) and hematocrit (% whole) in goldfish exposed to either cycling temperatures (circles) or constant temperature (squares). Open symbols, samples at 09:00 and 15:00; closed symbols, samples at 03:00 and 21:00. Values are means ± 1 SE. $N = 18$ in cycling temperature experiment.

(Bunn et al. 1971; de Bruin et al. 1974; Benesch and Benesch 1974; Rollema et al. 1975; Bonaventura et al. 1974; Weber and Lykkeboe 1978; Laver et al. 1977; Nigen et al 1980). Chloride acts much as do 2,3-DPG, ATP, and GTP, i.e. through introduction of additional salt bridges. The oxy−deoxyhemoglobin equilibrium relationship then favors the tense (or deoxygenated) state of the molecule. The oxygen equilibrium curve is shifted to the right and oxygen is released at higher tensions. Magnesium and calcium act through formation of nucleoside triphosphate complexes, which do not readily interact with hemoglobin. Consequently, increases in the red cell levels of these cations reduce effective concentrations of ATP and GTP. Because these are the principal organophosphate affinity modulators of fishes, hemoglobin–oxygen affinity is increased. Less is known regarding the effects of sodium and potassium. Both, however, reduce affinity, with potassium being the more effective of the two (Rossi-Fanelli et al. 1961; Bunn et al. 1971).

Under constant temperature conditions increases in temperature were associated with increases in cellular chloride levels and reductions in those of magnesium and calcium. Potassium levels tended to decrease whereas sodium was elevated. Such changes would be expected to reduce affinity and promote oxygen release under cirucumstances in which cellular oxygen requirements have been increased. A somewhat different situation was encountered with cycling temperature conditions. Cellular chloride and magnesium exhibited little variation in relation to time and temperature, and both remained at intermediate concentrations. Calcium was also stable, but well below the levels observed at constant temperature. Potassium and sodium exhibited trends similar to those seen under the latter conditions. Potassium concentrations were, however, higher in fish exposed to the cycle whereas sodium was lower.

In short, the goldfish appears to emphasize different features within a spectrum of possibly responses depending on the thermal regime to which it has been exposed. Under cycling conditions blood oxygen carrying capacity is raised and ionic concentrations within the red cell are stabilized. Under constant conditions hemoglobin levels increase with temperature and electrolyte levels are altered to reduce affinity as tissue oxygen requirements increase.

These observations are consistent with earlier reports (Houston 1980) suggesting that goldfish may invoke different forms of response at the hematological level to meet the respiratory demands of life at high temperature. Virtually all combinations of increases in hemoglobin content and red cell numbers, reductions in cell volume, and changes in hemoglobin system complement and the cellular conditions in which these hemoglobins function have now been described. The present study adds an additional variable. Unfortunately, at present little is known regarding either the nature or the mechanisms of action of the stimuli triggering specific elements of the response complex. Control of erythropoesis, for example, is poorly understood and thermal stimulation of red cell formation and hemoglobin synthesis in fishes has been seriously questioned (Denton and Yousef 1975). Recent studies on the recovery of goldfish from phenylhydrazine-induced anemia have shown that temperature does, in fact, stimulate erythrocyte production, but give little indication as to the mechanisms involved (J. Chudzik and A. H. Houston, Brock University, St. Catharines, Ont., unpublished data). Increases in chloride content can be correlated with increases in red cell (HCO_3^-)-stimulated ATPase and carbonic anhydrase activities (Houston and Mearow 1979, 1981). The stability of red cell chloride concentrations under cycling temperature conditions can also be related to reductions in the thermal dependence of erythrocytic carbonic anhydrase activity (Beaumont et al. 1981). Variations in carbonic anhydrase activity with temperature are of particular interest in the present context because increased export of HCO_3^- from the erythrocyte would tend to promote inward Cl^- movement. However, increases in red cell carbonic anhydrase activity cannot be accounted for solely in terms of thermal stimulation

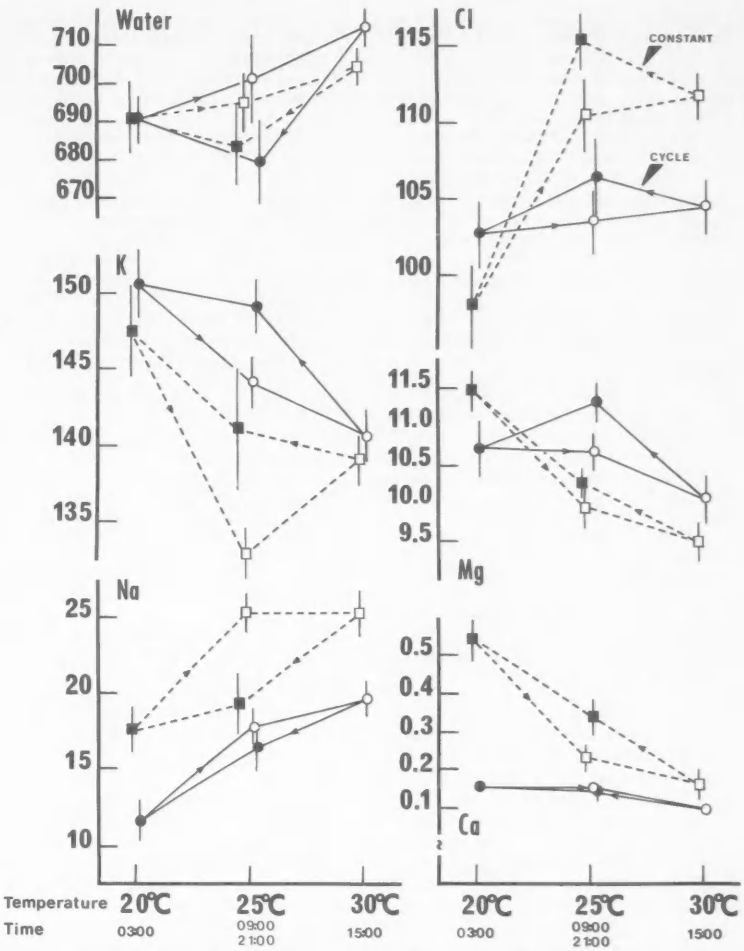

FIG. 2. Variations in red cell water content ($g \cdot kg^{-1}$) and potassium, sodium, chloride, magnesium, and calcium ($mmol \cdot L^{-1}$) in goldfish exposed either to cycling temperatures (circles) or constant temperature (squares). Open symbols, samples at 09:00 and 15:00; closed symbols, samples at 03:00 and 21:00. Values are means ± 1 SE. $N = 18$ in cycling temperature experiment.

(Houston and Mearow 1981; Beaumont et al. 1981). Accordingly, further studies will be required to clarify the nature of this apparently flexible form of physiological response.

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ANTHONY, E. H. 1961. The oxygen capacity of goldfish blood (*Carassius auratus*) in relation to thermal environment. J. Exp. Biol. 38: 93–107.

BEAMISH, F. W. H., AND P. S. MOOKHERJII. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. I. Influence of weight and temperature on the respiration of goldfish, *Carassius auratus* L. Can. J. Zool. 42: 161–175.

BEAUMONT, A.-L. T. F. KOSS, AND A. H. HOUSTON. 1981. Red cell carbonic anhydrase activity and chloride content in goldfish (*Carassius auratus* L.) exposed to constant and diurnally-cycling temperatures. Comp. Biochem. Physiol. (In press)

BENESCH, R., AND R. E. BENESCH. 1974. The mechanism of interaction of red cell organic phosphates with hemoglobin. Adv. Protein Chem. 28: 211–237.

BONAVENTURA, C., B. SULLIVAN, AND J. BONAVENTURE. 1976. Spot hemoglobin. Studies on the Root effect hemoglobin of a marine teleost. J. Biol. Chem. 251: 1871–1876.

BUNN, H. F., B. J. RANSIL, AND A. CHAO. 1971. The interaction between erythrocyte organic phosphates, magnesium ion and hemoglobin. J. Biol. Chem. 246: 5273–5279.

CATLETT, R. H., AND D. R. MILLICH. 1976. Intracellular and extracellular osmoregulation of temperature-acclimated goldfish, *Carassius auratus*. Comp. Biochem. Physiol. 55A: 261–269.

DE BRUIN, S. H., H. S. ROLLEMA, L. H. M. JANSSEN, AND G. A. J. VAN OS. 1974. The interaction of chloride ions with human hemoglobin. Biochem. Biophys. Res. Commun. 58: 210–215.

DENTON, J. E., AND M. K. YOUSEF. 1975. Seasonal changes in hematology of rainbow trout, *Salmo gairdneri*. Comp. Biochem. Physiol. 51A: 151–153.

FALKNER, N. W., AND A. H. HOUSTON. 1966. Some haematological responses to sublethal thermal shock in the goldfish, *Carassius auratus*. J. Fish. Res. Board Can. 23: 1109–1120.

FRY, F. E. J., J. R. BRETT, AND G. H. CLAWSON. 1942. Lethal limits of temperature for young goldfish. Rev. Can. Biol. 1: 50–56.

HOUSTON, A. H. 1980. Components of the hematological response of fishes to environmental temperature change: a review, p. 241–298. M. A. Ali [ed.] Proceedings NATO AS1, Environmental physiology of fishes. Plenum Publishing Corporation, New York, NY.

HOUSTON, A. H., AND D. CYR. 1974. Thermoacclimatory variation in the hemoglobin systems of goldfish (*Carassius auratus*) and rainbow trout (*Salmo gairdneri*). J. Exp. Biol. 61: 455–461.

HOUSTON, A. H., AND K. M. MEAROW. 1979. Temperature-related changes in the erythrocytic carbonic anhydrase (acetazolamide-sensitive esterase) activity of goldfish, *Carassius auratus*. J. Exp. Biol. 78: 255–264.

1981. Thermoacclimatory modification of red cell ionic composition in rainbow trout, *Salmo gairdneri:* possible relationship with (Na^+/K^+)- and (HCO_3^-)-stimulated ATPase activities. Comp. Biochem. Physiol. (In press)

HOUSTON, A. H., K. M. MEAROW, AND J. S. SMEDA. 1976. Further observations on the hemoglobin systems of thermally-acclimated freshwater teleosts: pumkinseed (*Lepomis gibbosus*), white sucker (*Catostomus commersoni*), carp (*Cyprinus carpio*), goldfish (*Carassius auratus*) and carp–goldfish hybrids. Comp. Biochem. Physiol. 54A: 267–273.

HOUSTON, A. H., AND R. RUPERT. 1976. Immediate response of the hemoglobin system of the goldfish, *Carassius auratus*, to temperature change. Can. J. Zool. 54: 1737–1741.

HOUSTON, A. H., AND J. S. SMEDA. 1979. Thermoacclimatory changes in the ionic microenvironment of haemoglobin in the stenothermal rainbow trout (*Salmo gairdneri*) and eurythermal carp (*Cyprinus carpio*). J. Exp. Biol. 80: 317–340.

HUGHES, G. M. 1964. Fish respiratory homeostasis, p. 81–107. *In* G. M. Hughes [ed.] Homeostasis and feedback mechanisms. The University Press, Cambridge.

LAVER, M. B., E. JACKSON, M. SCHERPERAL, C. TUNG, W. TUNG, AND E. P. RADFORD. 1977. Hemoglobin–O_2 affinity regulation: DPG, monovalent anions and hemoglobin concentrations. J. Appl. Physiol. Respir. Environ. Exercise Physiol. 43: 632–642.

LINN, D. W. 1965. Take a one gallon jar . . . . Prog. Fish Cult. 27: 147–152.

NIGEN, A. M., J. M. MANNING, AND J. O. ALBENS. 1980. Oxygen-linked binding sites for inorganic anions to hemoglobin. J. Biol. Chem. 255: 5525–5529.

ROLLEMA, H. S., S. H. DE BRUIN, L. H. M. JANSSEN, AND G. A. J. VAN OS. 1975. The effect of potassium chloride on the Bohr effect of human hemoglobin. J. Biol. Chem. 250: 1333–1339.

ROSSI-FANELLI, A., E. ANTONINI, AND A. CAPUTO. 1961. Studies on the relations between molecular and functional properties of hemoglobin. II. The effects of salts on the oxygen equilibrium of human hemoglobin. J. Biol. Chem. 236: 397–401.

SPOOR, W. H. 1951. Temperature and the erythrocyte count of goldfish. Fed. Proc. Fed. Am. Soc. Exp. Biol. 10: 131.

WEBER, R. E., AND G. LYKKEBOE. 1978. Respiratory adaptations in carp blood: influences of hypoxia, red cell organic phosphates divalent cations and CO_2 on hemoglobin–oxygen affinity. J. Comp. Physiol. 128: 127–137.

Parr–Smolt Transformation of Yearling Atlantic Salmon (*Salmo salar*) at Several Rearing Temperatures

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JOHNSTON, C. E., AND R. L. SAUNDERS. 1981. Parr–smolt transformation of yearling Atlantic salmon (*Salmo salar*) at several rearing temperatures. Can. J. Fish. Aquat. Sci. 38: 1189–1198.

Six different rearing conditions were used to study the effect of temperature on seasonal changes in growth, condition factor, body silvering, body moisture and lipid content, salinity tolerance, and gill Na–K-ATPase activities of laboratory and pond-reared yearling Atlantic salmon (*Salmo salar*). Growth during the winter was greatest at the highest rearing temperature (16°C) whereas those under simulated natural conditions grew slowest. Increasing temperatures in the spring stimulated growth more than constant temperature. Based on increased salinity tolerance, elevated ATPase activity, and growth in salt water, smolt development proceeded at all temperatures up to 16°C. More smolts were produced in the high thermal regimes resulting in the best growth and the largest proportion of fish reaching smolt size. Unlike some Pacific salmonids, Atlantic salmon develop smolt status at temperatures as high as 16°C. Yearling smolts can be produced at elevated temperatures and the use of thermal effluents for this purpose is promising.

Key words: smoltification, smolt criteria, salinity tolerance, ATPase activity, rearing temperatures, elevated thermal regimes, thermal effluent, *Salmo salar*

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Pour étudier les effets de la température sur les changements saisonniers de croissance, facteurs de condition, coloration argentée du corps, teneur en eau et en lipides corporels, tolérance à la salinité et activité de la Na–K-ATPase branchiale, nous avons soumis des saumons atlantiques (*Salmo salar*) d'un an élevés en laboratoire et en étangs à six conditions d'élevage différentes. La croissance en hiver est maximale à la température d'élevage la plus élevée (16°C), alors que les poissons soumis aux conditions naturelles simulées croissent le plus lentement. Des températures ascendantes au printemps stimulent la croissance plus qu'une température uniforme. À en juger par une tolérance accrue à la salinité, une activité plus grande de l'ATPase et la croissance en eau salée, le développement des smolts se poursuit à toutes températures jusqu'à 16°C. Un plus grand nombre de smolts ont été produits à de hautes températures, avec, comme résultat, la meilleure croissance et la plus forte proportion de poissons atteignant la taille de smolt. Contrairement à certains salmonidés du Pacifique, le saumon atlantique se transforme en smolt à des températures aussi élevées que 16°C. Des smolts âgés d'un an peuvent être produits à des températures élevées, et l'utilisation d'effluents thermiques à cette fin est prometteuse.

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PHOTOPERIOD and temperature are important external factors controlling the onset and development of smoltification in salmonids (Adams et al. 1973; Clarke and Shelbourn 1977; Clark et al. 1981; Hoar 1965; Johnston and Eales 1967, 1968, 1970; Knutsson and Grav 1976; Komourdjian et al. 1976a; Saunders and Henderson 1970, 1978; Wedemeyer et al. 1980; Wagner 1974; Zaugg et al. 1972; Zaugg and Wagner 1973). When photoperiod and temperature are in phase, a maximal smolting response occurs (Wagner 1974). However, in some salmonids some aspects of the smolting response are greatly retarded by water temperatures above 13°C (Adams et al. 1973, 1975; Harache et al. 1980; Wagner 1974). This retardation is of particular interest because some aquaculture operations use heated culture water to produce 1-yr smolts (Gudjonsson 1973; Peterson 1973; Knutsson and Grav 1976; Goff and Forsyth 1979; Saunders 1976). The effect of ele-

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vated water temperature on smolt physiology has not been clearly described for Atlantic salmon (*Salmo salar*). Therefore, we examined the effect of six thermal regimes on seasonal changes in growth, condition factor, body silvering, body moisture and lipid content, salinity tolerance, and ATPase activities of laboratory and pond-reared yearling Atlantic salmon.

Materials and Methods

Salmon Stock and Culture Conditions

On September 11, 1979, 2000 Atlantic salmon parr of Saint John River stock were transported to the St. Andrews Biological Station. Salmon were held in two tanks under ambient temperature and simulated natural photoperiod conditions until October 6, when three groups of 358 parr were randomly selected, weighed, measured for fork length, and transferred to 1-m^2 Swedish-type center-draining Fiberglas tanks which were filled to a depth of 25−27 cm with flowing dechlorinated freshwater. Three thermal regimes were initiated: an advanced cycled temperature regime (AT) in phase with photoperiod in which water temperature was lowered from 15°C in October to 4°C by mid-December, whereupon it was slowly increased to 13°C by late May; a delayed cycled temperature regime (DT) out of phase with photoperiod in which water temperature was lowered from 15°C in October to 4°C by mid-February, whereupon it was increased to 12°C by June; and a constant 16°C regime (16T) (Fig. 1). Two other temperature regimes were set up later in the experimental period: a constant 10°C regime (10T) in December and a 16−8°C cycled temperature regime (16−8T) in March (Fig. 1).The 330 salmon placed in the 10T regime in December were maintained from September to late November at the Saint John Fish Culture Station under prevailing temperature and photoperiod conditions. They were later transferred to St. Andrews for this experiment. The 40 salmon placed in the 16−8T regime in March were from the 16T population. Unlike the other groups, salmon in the 16T regime were cultured in a recirculated water system (Henderson and Saunders 1978) instead of fresh running water because of anticipated difficulties in maintaining a 16 ± 0.5°C temperature during the winter months.

Flow rates in each culture tank were maintained between 6 and 9 $L \cdot min^{-1}$ and water temperatures within ± 0.2°C. Overhead lighting was by fluorescent bulbs controlled by astral timers set to give a simulated natural photoperiod (Fig. 1). Screens of 0.5-cm round mesh netting were placed on top of each tank to prevent salmon from jumping out. Light intensities at the water surface were 430−538 lx. During the experimental period dissolved oxygen, ammonia levels, and pH in the AT, DT, 10T, and 16−8T regimes were 85−100% of air saturation, 0.086−0.497 $mg \cdot L^{-1}$, and 6.58−6.80, respectively. In the 16T regime the respective levels were 52−75%, 1.329−2.160 $mg \cdot L^{-1}$, and 6.27−6.82. All salmon were fed daily on Silver Cup dry pellet salmon feed in graded sizes having a crude protein content of 48%, fat 8%, fiber 5%, and ash 17%. The daily food ration for each tank was set at 5% of the total wet body weight per day of the heaviest group of salmon at each monthly weighing. A weighed daily ration was placed in automatic feeders each morning and released at 45-min intervals throughout the day.

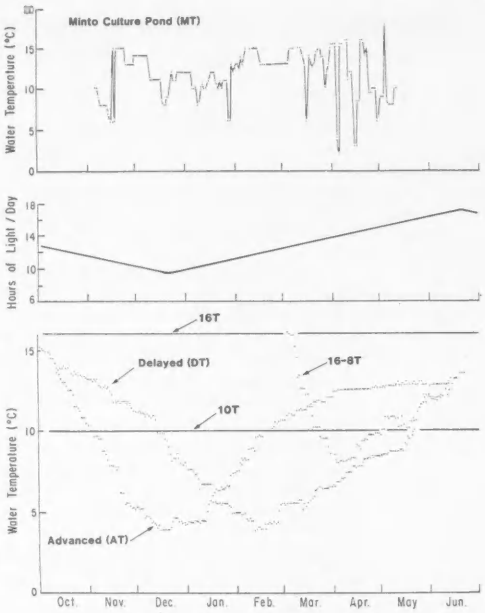

FIG. 1. Changes in daily temperature and photoperiod for the five rearing conditions in St. Andrews. Water temperatures at the inflow at Minto are also shown.

A final experimental group (MT) of 30 000 Atlantic salmon of the same Saint John River stock was cultured from November 5, 1979, in an outdoor pond receiving thermal effluent from the coal-fired Grand Lake Generating Plant at Minto, N.B. The pond was 60 × 30 × 1.2 m and had a Hypalon rubber liner. Heated effluent was pumped at a rate of 387 000 $L \cdot min^{-1}$ over wooden nitrogen degassers before entering the pond. The pond volume was completely exchanged every 5.5 h. Water temperatures at the inflow were maintained between 6 and 10°C during November, December, and January, and between 13 and 15°C between February and May (Fig. 1). Water temperatures in the culture pond were from 1 to 5°C lower at the outflow than at the inflow owing to air temperature and wind conditions. On several occasions the power plant was shut down and the temperature fell to even lower levels. Salmon were fed Silver Cup dry pellets with a daily ration of 3−4% wet body weight per day.

Growth Measurements

At the beginning of each month all salmon reared in AT, DT, 10T, 16T, and 16−8T were starved for 24 h, anesthetized with 1−3% tertiary amyl alcohol, weighed, and measured (fork length). Instantaneous growth rates were calculated for length and weight using the equation:

$$\text{instantaneous growth rate} = \frac{\log_e Y_{T_2} - \log_e Y_{T_1}}{T_2 - T_1}$$

where Y was the mean length or weight at times T_2 and T_1, T_2 being later than T_1.

In the MT regime, 350 salmon were randomly seined each month from different locations in the culture pond. They were also anesthetized, weighed, and measured. Before returning the 350 salmon to the culture pond, three subsamples, each of 10 salmon, representing large, medium, and small fish in the population were removed and taken to St. Andrews for lipid and ATPase assays and salinity tolerance tests. At St. Andrews they were held in running freshwater at the prevailing MT temperature for at least 24 h before being assayed.

Moisture and Lipid Assays

Ten salmon, representing the full size range in each regime, were killed with a lethal dose of anesthetic, weighed, measured, sexed, and the body cavity opened midventrally. The moisture content of each salmon carcass was determined by drying it to a constant weight in a forced draft oven at 80°C for 48 h. Moisture content was expressed as percentage fresh body weight.

Lipid assays were conducted on the total dried and weighed carcass. Each carcass was blended to a fine consistency using a 50-mL Waring blender and extracted with 100 mL hexane (99% mole pure)−isopropanol (3:2) for 2−4 h (Hara and Radin 1978). The mixture was filtered through a medium fritted glass filter with pressure. Tissue and equipment were washed several times with the extracting solvent until the tissue to solvent ratio approached 1 g of dry tissue to 18 mL solvent. Nonlipids in the extract were removed by shaking 100 mL of 6.7% warm sodium sulfate with the extracting solvent in a separatory funnel for several minutes. The lipids in the upper hexane-rich layer were easily separated from the aqueous lower layer. The hexane-rich layer was transferred to a preweighed petri dish, evaporated to dryness in an airstream, and later dried to a constant weight in a forced draft oven at 80°C for 2−4 h. The lipid content was expressed as a percentage of the dry weight of each carcass.

Salinity Tolerance Tests

At different times during the experimental period, 10 salmon, representing the full size range in each regime, were selected and tested for tolerance to seawater (35‰ salinity). Tests were conducted in 68 × 48 × 36 cm tanks with screened tops. The water temperature of each salinity test was the same as that for each freshwater regime at the time of testing. During each 96-h test the water temperature was kept constant and mortalities were recorded every 2 h. Dead salmon were weighed, measured (for length), and sexed. Salmon surviving the test were held in a 1-m^2 tank in flowing seawater (28−29‰ salinity) until the experiment was terminated.

Gill ATPase Assays

The ATPase assay was modified from the procedures of Saunders and Henderson (1978). For each assay, 10 salmon representing the full size range in each regime were sampled monthly from January to June. Each sample was segregated from the tank population in buckets with flowing aerated freshwater for at least 24 h prior to the assay. On the day of the assay the salmon were transferred to a 2−4°C constant temperature room where each was killed by a blow to the head, weighed, measured, sexed, and bled from the caudal peduncle. The gill arches and gill filaments were removed and washed in a volume of ice-cold 250 mmol·L^{-1} sucrose−5 mmol·L^{-1} ethylenediaminetetraacetic acid (EDTA). The filaments were blotted, cut from the gill arches, and weighed to the nearest milligram. Excised filaments were homogenized in sucrose−EDTA solution (the ratio of tissue to solvent was 36 mg wet gill tissue per millilitre sucrose−EDTA) with a motor-driven rotating Teflon pestle at 0°C. The homogenate was frozen in liquid nitrogen for more than 30 min and stored at −80°C until enzyme assays were carried out. All assays were completed within 2 wk of tissue preparation.

On the day of the enzyme assay the frozen homogenate was quickly thawed in a warmwater bath and held at 0°C. To prevent tissue sedimentation, the homogenate was stirred vigorously before each sampling. A 0.2-mL aliquot of the homogenate was added to each of three tubes containing 0.1 mL of 1000 mmol·L^{-1} NaCl−200 mmol·L^{-1} KCl−2 mmol·L^{-1} ouabain and 0.5 mL of Tris buffer (pH 7.6), and to each of three tubes containing 0.1 mL of 1000 mmol·L^{-1} NaCl−200 mmol·L^{-1} KCl and 0.5 mL of 200 mmol·L^{-1} Tris buffer (pH 7.6). All tubes were preincubated for 5 min at 37°C. The reaction was started by adding 0.2 mL of 30 mmol·L^{-1} ATP (disodium salt) in a 25 mmol·L^{-1} $MgCl_2$ solution at 37°C and stopped in exactly 10 min by adding 4 mL of cold 1% ammonium molybdate in 0.57 mol·L^{-1} H_2SO_4 into which 40 mg·mL^{-1} ferrous sulfate had been dissolved just before use. Samples were centrifuged for 3−5 min at 5000 rpm and the blue color of the reaction mixture was allowed to develop for 1 h before the absorbancy of each sample was measured at 700 nm.

The amount of phosphate liberated from ATP during the reaction period was expressed as the number of μmol P_i·mg protein^{-1}·h^{-1}. The protein content of the homogenate was determined in duplicate using a modification of the Lowry method (Hartree 1972). Absorbancies were read at 650 nm and bovine serum albumin was used as a protein standard. Statistical comparisons were made using Duncan's multiple range test.

Results

Growth

Growth of salmon in the different regimes was related directly to rearing temperature (Table 1). During the fall and winter salmon had higher growth rates in 16T than in any of the other conditions. Salmon had the lowest growth rates in AT where water temperature was low. With increasing photoperiod and temperature in the spring, growth rates of salmon in both AT and 10T increased, with AT exceeding those of 16T in March, April, and May, and 10T only in March.

TABLE 1. Mean fork length ($\overline{FL}$) in cm, weight ($\overline{WT}$) in g, coefficient of condition ($\overline{CF}$), and instantaneous growth rate in length (G_L) and weight (G_W) $\times 10^{-2}$. N represents the number of salmon in each temperature regime.

	DT						10T						AT					
Period	N	$\overline{FL}$	$\overline{WT}$	$\overline{CF}$	G_L	G_W	N	$\overline{FL}$	$\overline{WT}$	$\overline{CF}$	G_L	G_W	N	$\overline{FL}$	$\overline{WT}$	$\overline{CF}$	G_L	G_W
October	358	7.97	4.76	0.91	—	—	—	—	—	—	—	—	358	8.02	4.84	0.91	—	—
November	347	8.35	5.53	0.90	0.179	0.577	—	—	—	—	—	—	354	8.36	5.54	0.91	0.143	0.466
December	321	9.17	8.09	0.97	0.283	1.153	330	8.60	6.15	0.96	—	—	331	8.60	6.29	0.95	0.088	0.397
January	306	9.82	10.46	1.01	0.228	0.856	320	8.64	6.32	0.92	0.021	0.124	319	8.76	6.78	0.97	0.061	0.250
February	270	10.12	11.77	1.03	0.100	0.393	288	8.97	7.37	0.97	0.125	0.512	269	8.99	7.75	1.02	0.086	0.446
March	237	10.38	12.78	1.05	0.082	0.266	257	10.49	13.14	1.09	0.505	1.865	236	10.65	13.70	1.09	0.547	1.838
April	207	11.08	15.56	1.06	0.233	0.703	227	12.00	19.73	1.09	0.480	1.451	205	12.73	24.41	1.13	0.637	2.063
May	166	12.99	24.54	1.06	0.442	1.266	197	13.75	30.04	1.12	0.378	1.168	173	15.46	43.86	1.16	0.525	1.584

	16T						16-8T						MT					
Period	N	$\overline{FL}$	$\overline{WT}$	$\overline{CF}$	G_L	G_W	N	$\overline{FL}$	$\overline{WT}$	$\overline{CF}$	G_L	G_W	N	$\overline{FL}$	$\overline{WT}$	$\overline{CF}$	G_L	G_W
October	358	7.89	5.00	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—
November	356	8.32	5.71	0.96	0.231	0.577	—	—	—	—	—	—	—	—	—	—	—	—
December	330	9.69	9.72	0.99	0.448	1.565	—	—	—	—	—	—	330	8.60	6.32	0.96	—	—
January	310	11.31	17.28	1.06	0.515	1.918	—	—	—	—	—	—	350	9.08	8.42	1.02	0.151	0.797
February	275	13.20	28.65	1.09	0.533	1.743	—	—	—	—	—	—	350	9.98	10.90	1.02	0.262	0.717
March	199	15.11	43.14	1.12	0.436	1.320	—	—	—	—	—	—	349	12.20	22.24	1.07	1.112	3.962
April	124	17.70	71.15	1.20	0.565	1.787	40	16.60	58.08	1.12	0.336	3.428	—	—	—	—	—	—
May	83	20.85	104.95	1.13	0.486	1.111	20	19.60	82.40	1.00	0.449	0.945	850[a]	13.20	26.70	1.10	0.141	0.326
													150	17.80	56.10	0.97	—	—
													1000	13.90	31.13	1.03	0.233	0.600

[a]One thousand salmon were measured at Minto; 850 were randomly selected from the population and 150 were randomly selected from 3000 known smolts.

TABLE 2. Mean fork length ($\overline{FL}$) and weight ($\overline{WT}$) of salmon before transfer to seawater of 28−29‰ salinity (May 12 and 26) and 44 and 58 d after transfer. *N* represents the number in each group and values in parentheses are ranges.

	May 26			July 8			Mortalities[a]		
Condition	*N*	$\overline{FL}$	$\overline{WT}$	*N*	$\overline{FL}$	$\overline{WT}$	*N*	$\overline{FL}$	$\overline{WT}$
AT	51	16.4 (12.6−20.9)	52.6 (23.0−95.9)	35	18.0 (12.6−23.6)	65.0 (21.0−134.3)	16	15.4 (12.7−18.2)	38.2 (17.2−61.8)
DT	66	13.8 (10.5−18.3)	30.8 (16.1−69.5)	55	14.1 (10.5−18.3)	31.5 (11.4−61.1)	11	13.6 (11.5−17.8)	27.6 (18.5−53.1)
10T	122	14.3 (9.2−19.8)	34.6 (8.4−82.2)	57	15.4 (13.1−22.4)	40.8 (24.3−120.9)	65	13.2 (9.2−18.2)	23.2 (7.0−61.8)
	May 12			July 8					
16T	9	21.2 (17.1−24.4)	100 (50.7−147.4)	9	22.3 (17.5−25.5)	113.4 (103.1−168.8)			
16−8T	5	21.2 (20.5−22.0)	95.5 (92.9−103.8)	5	24.6 (22.5−25.6)	158.1 (110.0−184.7)			

[a]Represents fish that died at various times during the 44-d exposure to seawater.

TABLE 3. Number, fork length range, and percentage of parr, silvery parr, and smolts in each temperature regime on May 26, 1980.

Condition		Parr	Silvery parr	Smolt
AT	Number	—	85	48
	Fork length range (cm)	—	13.1−17.9	15.2−20.8
	%	—	64	36
DT	Number	4	109	27
	Fork length range (cm)	9.5−11.6	10.5−14.3	12.1−20.0
	%	3	78	19
10T	Number	1	153	12
	Fork length range (cm)	9.2	11.0−17.1	16.2−19.9
	%	1	92	7
16T	Number	—	2	32
	Fork length range (cm)	—	17.1−21.7	16.3−25.0
	%	—	7	93
16−8T	Number	—	3	12
	Fork length range (cm)	—	13.5−13.7	14.2−23.3
	%	—	20	80

Therefore, increasing water temperature in January and February influenced growth more than increasing temperature in March or April or by maintaining a constant 10°C temperature. Growth rates of salmon in May leveled off or declined in most regimes and this change was coincident with smolting.

The mean condition factor for salmon under each regime generally increased throughout the experimental period. The condition factor was generally higher for salmon in 16T than in any other regime. There was no apparent trend associated with smolting.

Growth and mortality of salmon in seawater of 28−29‰ following slow acclimation (5 d) in late May were measured after 44 and 58 d (Table 2). Salmon from 16−8T, AT, and 10T regimes grew the most and those from DT the least. Mortality was highest in the 10T and AT groups and lowest in DT. Whereas some salmon may have died from dehydration and inability to osmoregulate, others may have died from *Vibrio* as integumentary lesions were evident on three carcasses from the MT regime in May.

BODY SILVERING

On May 26, 1980, the degree of body silvering was visually assessed as to parr (obvious parr marks and little silvering), silvery parr (some parr marks with silvering), or smolts (complete body silvering, no parr marks with darkened fin margins) for the salmon in each regime (Table 3). There was a higher percentage of salmon with silvery color in the 16T and 16−8T than in any of the other regimes. Silvering in these two groups was well advanced by early March such that many of the larger salmon had the appearance of smolts. Although they had the appearance of smolts, they were not tolerant to seawater of 35‰ salinity. Such tolerance was not fully developed until May.

Parr with various degrees of silvering remaining in each regime at the end of May were slowly acclimated to 28−29‰ salinity over 5 d. In each regime many silvery parr became more silvery and eventually developed a smolt-like appearance.

TOTAL BODY LIPID AND MOISTURE

Total body lipid for the AT, DT, 10T, and MT groups decreased until January or February and then steadily increased until May (Fig. 2). In each regime the January or February lipid level was significantly lower ($P < 0.05$) than the values for November or April and May. Increases in body lipid were accompanied by decreases in body moisture. In all cases the coefficient of condition followed the pattern of total body lipid. Because each sample consisted of salmon of dif-

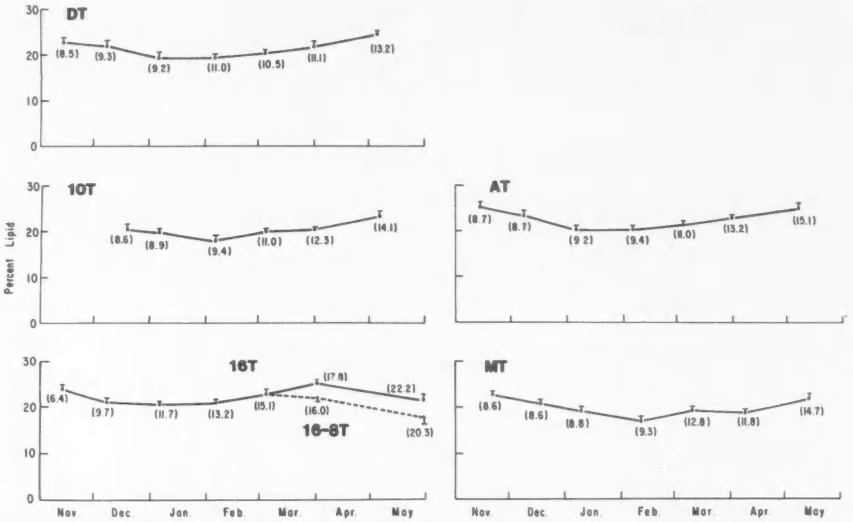

FIG. 2. Changes in total body lipid for salmon in the experimental regimes (DT, delayed temperature; AT, advanced cycled temperature; 10T, constant 10°C; MT, temperatures at Minto rearing ponds; 16T, constant 16°C; and 16−8T, cycled temperature in March). Each point represents a mean (+ or −SE) of 10 determinations. Mean fork lengths are shown in parentheses.

ferent sizes and states of smolting, a marked decrease in lipid was not evident in most groups by May. However, in any regime, if only those salmon with low condition factors are considered, lipid levels declined as much as 5−10%, particularly for large smolting fish. More obvious declines in lipid content were recorded for the 16T and 16−8T groups (Fig. 2). Salmon in the 16−8T group had significantly lower lipid and condition factor than those in 16T ($P < 0.05$). Lipid levels for salmon in the 16T group, however, were not markedly lower than the levels for other groups.

SALINITY TOLERANCE AND ATPASE ACTIVITY

Seasonal changes in the tolerance of salmon to 35‰ salinity varied for the different experimental regimes (Table 4). Salmon in AT, 10T, and MT regimes appeared to develop salinity tolerance earlier than salmon in DT, 16T, or 16−8T. With the exception of the 16T group, this increased tolerance appeared related to both size and temperature. Increasing rearing temperatures in phase with increasing photoperiod in accordance with natural cycles (DT May 7) produced greater tolerance in smaller salmon than increasing (AT, MT) or constant (10T) temperature regimes out of phase with photoperiod. High constant rearing temperatures (16T) appeared to inhibit salinity tolerance until May, but a large body size facilitated the development of euryhalinity. Lowering the water temperature from 16 to 8°C and bringing it in phase with a natural cycle also enhanced the development of salinity tolerance in these larger salmon.

Generally, in all regimes, Na−K-ATPase activity was linearly related to body size, with larger salmon having higher ATPase levels earlier than smaller ones. No attempt was made to correct for differences in body size because size was a function of the experimental condition and all size groups were sampled in each regime.

Na−K-ATPase activity peaked in April for salmon in 10T, AT, and MT, but not until May and June for DT, 16T, and 16−8T (Fig. 3). Statistical comparisons of the data for the different regimes showed that the following were significantly different ($P < 0.05$):

Jan.−Mar.	Na−K-ATPase levels not significantly different among regimes
Early Apr.	16−8T not significantly greater than 16T
Mid Apr.	16−8T significantly greater than 16T, 10T, MT
Late Apr.	MT smolts (large smolts, mean fork length 20.4 cm (Fig. 3)) significantly greater than MT, 10T, 16T in early May
Early May	DT significantly greater than AT and MT
Late May	16T, 16−8T, DT significantly greater than 10T, AT, and MT
June	16−8T significantly greater than 16T and DT; 16T significantly greater than DT

Naturally increasing temperature in spring in phase with an increasing photoperiod cycle produced the greatest increase in Na−K-ATPase activity. Although high ATPase activity was found to occur in late May in salmon reared at 16°C, this period of heightened activity was of very short duration. In contrast, when 16°C salmon were cycled down in temperature and brought into phase with a more natural temperature regime, a maximal response was induced which persisted until late June.

Natural photoperiod and lighting conditions, combined with fluctuating high temperatures (MT), produced smolts by late April or early May. A sample of these larger smolts (mean

TABLE 4. Effect of rearing conditions on tolerance of Atlantic salmon to 35‰ seawater from November to late May (mean fork length of 10 salmon in each test).

Date	Time (h) to 50% mortality[a] in 35‰ seawater					
	DT	AT	10T	16T	16−8T	MT
Nov.	5.6	11	—	0.6	—	8
	(8.4)	(8.5)		(8.1)		(8.3)
Jan.	12.5	12.5	9.2	12	—	—
	(12.2)	(8.8)	(9.5)	(10.0)		
Feb.	18	13.2	14	16	—	—
	(10.4)	(8.8)	(9.3)	(12.8)		
Mar.	20	34	70	38	—	30
	(10.3)	(10.7)	(10.8)	(15.0)		(12.6)
Apr.	38	72	>100	38	—	65
	(10.7)	(13.2)	(12.2)	(16.8)		(11.9)
May 7	>100	80	70	>100	>100	52[b]
	(13.0)	(15.1)	(13.5)	(21.2)	(21.2)	(14.2)
May 27	68	74	96	—	—	—
	(13.5)	(16.5)	(14.0)			

[a]Time to 50% mortality determined from probit plots (Finney 1952).
[b]Ten smolts were tested May 5, 1980; mean fork length 20.4 cm, $LT_{50} > 100$.

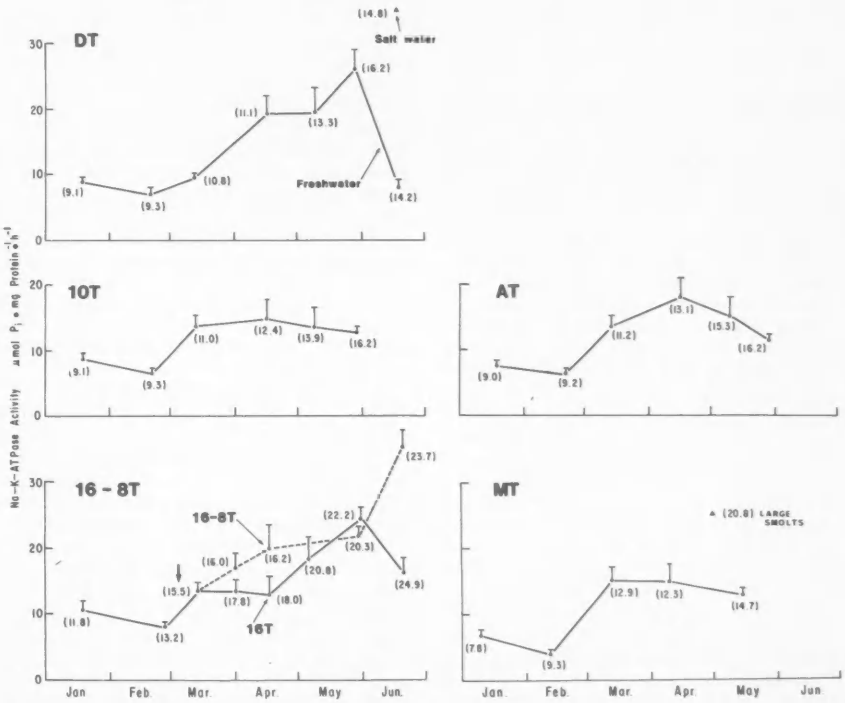

Fig. 3. Changes in Na−K-ATPase activity for salmon in the experimental regimes. Each point represents a mean (±SE) of 10 determinations. Mean fork lengths are shown in parentheses.

fork length 20.8 cm) had mean Na−K-ATPase activity over 25 µmol P_i·mg protein^{-1}·h^{-1}, and all survived the salinity tolerance test (Table 4). In comparison with the other groups, irregular fluctuations in temperature appear to have induced a more marked degree of smolting, particularly in the larger salmon, and high rearing temperatures did not inhibit seasonal increases in ATPase activity.

Toward the end of May salmon remaining in each regime

were slowly acclimated to 28−29‰ seawater. After 23 d in seawater, Na−K-ATPase activity was measured in salmon from the DT regime and found to be significantly higher ($P < 0.05$) than for those in freshwater, even though the condition factor was not markedly different from the two groups (salt water 0.99; freshwater 1.04).

Residual ATPase activity (Mg-ATPase and any other ATPase not inhibited by ouabain) showed slight seasonal variations but these did not appear to be related to rearing conditions.

Discussion

Changes in lipid- moisture levels, body−fin coloration, salinity tolerance, and gill Na−K-ATPase activity show that yearling Atlantic salmon undergo the parr−smolt transformation when reared at temperatures up to 16°C. Whereas the percentage of body lipid and body moisture changed in a reciprocal pattern similar to that described by Saunders and Henderson (1978), the extent of lipid change was much less than previously reported by them. The lack of an obvious decline in lipid, a characteristic of smolting salmon, was probably due to sampling and feeding. Salmon drawn for lipid assays represented small, medium, and large fish in each population and therefore consisted of smolting and non-smolting salmon. Nonsmolting salmon would tend to reduce the extent of lipid change and mask the effects associated with smolting. In addition to this, a heavy feeding schedule (5% wet body weight per day) may have contributed to a greater food intake prior to and during smolting, thereby counteracting increased metabolic demand and subsequent depletion of body lipid reserves.

In all regimes, gill Na−K-ATPase activity increased during the spring similar to that described by McCartney (1976) and Saunders and Henderson (1978). In this study, maximum ATPase activity was reached in late April in AT, 10T, and MT regimes and 1 mo later in 16T, 16−8T, and DT regimes. Salmon reared at 16°C developed elevated ATPase activity for only a brief period in late May and then quickly declined to presmolt levels in June. These results are similar to those described for coho salmon (*Oncorhynchus kisutch*) in which rearing temperatures of 15 and 20°C also caused ATPase activity to become elevated for a brief period in the spring (Zaugg and McLain 1976). In another study, a rearing temperature of 12°C was shown to have no effect on ATPase activity or smolting in chinook salmon (*O. tshawytscha*) (Ewing et al. 1979). However, rearing temperatures above 13°C were shown to prevent spring increases in ATPase activity and euryhalinity in smolting steelhead trout (*Salmo gairdneri*)(Adams et al. 1973, 1975). ATPase activity in steelhead trout appears to be more inhibited by elevated temperatures during the parr−smolt transformation than in either coho, chinook, or Atlantic salmon.

Although the smolting period in salmon reared at 16°C is short, it may be prolonged by reducing culture temperatures early in spring to bring salmon in phase with a more natural temperature condition. Such a combination of rearing conditions produced smolts showing more typical changes in condition factor, lipid content, coloration, and ATPase activity, and better growth in salt water.

Although salmon cultured in the DT regime had higher gill ATPase activity and lower mortality in seawater than salmon in the other regimes, growth during the 44-d period in seawater was lower. These data suggest that smaller salmon take longer to adapt to seawater than larger fish even though their ATPase levels are high. The high surface to volume ratio in small fish or their lack of smolt status may be the reason for this slow adaptation. Seawater tolerance in salmonids has been shown to be a function of size (Elson 1957; Parry 1960; Houston 1961; Conte et al. 1966; Wagner et al. 1969). Farmer et al. (1978) have demonstrated that euryhalinity may be achieved when Atlantic salmon reach a fork length of 12−13 cm. Our results, with the exception of the 16T group, support these findings. At high rearing temperatures, euryhalinity is suppressed until salmon are much larger, developing only when endogenous smolting cycles peak in May.

Salmon survive 28−29‰ seawater before many of the smolt characteristics, such as complete body silvering, low body lipid, high body moisture, and high Na−K-ATPase activity, are fully developed. Evidently such changes are not essential prerequisites to survival in seawater. Indeed, salmon parr of 10−12 cm can live for long periods in 30‰ seawater, especially at low temperatures (Saunders and Henderson 1969; Komourdjian et al. 1976b). Therefore, which criteria are the best indicators of smolt status? Based on this study, gill Na−K-ATPase activity together with growth in seawater appear to be the better criteria for judging smolt status. In situations where it is not practical to measure ATPase activity, salinity tolerance tests in 40‰ salinity appear to provide a good criterion of smolt condition (Komourdjian et al. 1976a; Saunders and Henderson 1978).

Although exposure to 28−29‰ seawater in late May caused high mortality in both AT and 10T regimes, this mortality could probably have been reduced by an earlier transfer to salt water. Transferring salmon to salt water when gill Na−K-ATPase activity is declining appears to cause a more marked mortality than when it is increasing. Therefore the best time for transfer appears to be as enzyme activity is increasing in the spring.

The size of smolts and their timing of entry into salt water may be important determinants in producing adult returns. Ritter (1972) has shown that the rate of adult return increases with increasing fork length at release up to a size of 19 cm. Beyond this length the percent return from yearling smolts declines rapidly. Such poor returns of smolts may be related to the timing of releases coinciding with declining gill Na−K-ATPase activity rather than to their large size. This suggests that the timing of increased ATPase activity may be different and that high activity may persist for different times in larger than in smaller smolts. Indeed, smolts grown under a high temperature regime, reaching a large size and having an early rise in ATPase activity (such as our 16−8T fish), might best be released earlier than smolts produced in lower temperature regimes. Thermal regimes in nature and at hatcheries probably result in different times of peak ATPase activity and therefore call for different release times. Further studies are needed to investigate the possible relationship between the timing of maximal ATPase activity and migratory behavior in different sized salmon reared under natural and hatchery conditions.

The use of heated effluents for the culture of salmonids has been steadily increasing, particularly in systems for intensive aquaculture (Mathiasson 1970; Peterson et al. 1972; Gudjonsson 1973; Isaksson 1976; Saunders 1976; Carroll et al. 1980; Sumari and Westman 1980; Tuunainen et al. 1980; Virtanen et al. 1980). In the United States and Canada, generating plants discharge large volumes of heated effluent. Carroll et al. (1980) estimate that the volume of heated effluent discharged in the United States each year is ~15% of the total United States river and stream flow. Such volumes of heated effluent could be more effectively used for the production of food. Peterson (1973) points out that the production cost of 1-yr-old smolts is considerably lower than for older smolts and that fast-growing salmon are more resistant to diseases and parasites. These facts are particularly important in intensive aquaculture operations, and this study demonstrates that it is possible to use heated effluents to accelerate the growth of juvenile salmon without suppressing the parr–smolt transformation.

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ADAMS, B. L., W. S. ZAUGG, AND L. R. MCLAIN. 1973. Temperature effect on parr–smolt transformation in steelhead trout (*Salmo gairdneri*) as measured by gill sodium–potassium stimulated adenosine triphosphatase. Comp. Biochem. Physiol. 44A: 1333–1339.

1975. Inhibition of salt water survival and Na–K ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Trans. Am. Fish. Soc. 104: 766–769.

CARROLL, B. B., W. A. HUBERT, AND R. L. WARDEN. 1980. Flow-through systems/North America. European Inland Fisheries Advisory Commission (EIFAC)/80/Symp:R/18. 15 p. (FAO, Rome.)

CLARKE, W. C., AND J. E. SHELBOURN. 1977. Effect of temperature, photoperiod and salinity on growth and smolting of underyearling coho salmon. Am. Zool. 17: 957.

CLARKE, W. C., J. E. SHELBOURN, AND J. R. BRETT. 1981. Effect of artificial photoperiod cycles, temperature, and salinity on growth and smolting in underyearling coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), and sockeye (*O. nerka*) salmon. Aquaculture 22: 105–116.

CONTE, F. P., H. H. WAGNER, J. FESSLER, AND C. GNOSE. 1966. Development of osmotic and ionic regulation in juvenile coho salmon *Oncorhynchus kisutch*. Comp. Biochem. Physiol. 18: 1–15.

ELSON, P. F. 1957. The importance of size in the change from parr to smolt in Atlantic salmon. Can. Fish Cult. 21: 1–6.

EWING, R. D., S. L. JOHNSON, H. J. PRIBBLE, AND J. A. LICHATOWICH. 1979. Temperature and photoperiod effects on gill (Na+K)-ATPase activity in chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 36: 1347–1353.

FARMER, G. J., J. A. RITTER, AND D. ASHFIELD. 1978. Seawater acclimation and parr–smolt transformation of juvenile Atlantic salmon *Salmo salar*. J. Fish. Res. Board Can. 35: 93–100.

FINNEY, D. J. 1952. Probit analysis. 2nd edition. Cambridge University Press, London and New York.

GOFF, T. R., AND L. S. FORSYTH. 1979. Production of Atlantic salmon smolts in one year without artificial heating of water, Mersey Hatchery, Nova Scotia. Fish. Mar. Serv. Tech. Rep. 841. 13 p.

GUDJONSSON, T. 1973. Smolt rearing techniques, stocking and tagged adult recaptures in Iceland. Int. Atl. Salmon Found. Spec. Publ. Ser. 4: 227–235.

HARA, A., AND N. S. RADIN. 1978. Lipid extraction of tissues with a low toxicity solvent. Anal. Biochem. 90: 420–426.

HARACHE, Y., G. BOEUF, AND P. LASSERRE. 1980. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. III. Survival and growth of juvenile coho salmon transferred to sea water at various times of the year. Aquaculture 19: 253–273.

HARTREE, E. F. 1972. Determination of protein: a modification of the Lowry method that gives a linear photometric response. Anal. Biochem. 48: 422–427.

HENDERSON, E. B., AND R.L. SAUNDERS. 1978. Comparative growth of rainbow trout reared in recycle and single pass system. Int. Counc. Explor. Sea, C.M.1978/F:20. 10 p.

HOAR, W. S. 1965. The endocrine system as a chemical link between the organism and its environment. Trans. R. Soc. Can. 3: 175–200.

HOUSTON, A. H. 1961. Influence of size upon the adaptation of steelhead trout (*Salmo gairdneri*) and chum salmon (*Oncorhynchus keta*) to sea water. J. Fish. Res. Board Can. 18: 401–415.

ISAKSSON, A. 1976. Preliminary results from the 1973 tagging experiments at the Kollafjördur experimental fish farm. J. Agric. Res. Icel. 8, 1–2: 14–18.

JOHNSTON, C. E., AND J. G. EALES. 1967. Purines in the integument of the Atlantic salmon (*Salmo salar*) during parr–smolt transformation. J. Fish. Res. Board Can. 24: 955–964.

1968. Influence of temperature and photoperiod on guanine and hypoxanthine levels in skin and scales of Atlantic salmon (*Salmo salar*) during parr–smolt transformation. J. Fish. Res. Board Can. 25: 1901–1909.

1970. Influence of body size on silvering of Atlantic salmon (*Salmo salar*) at parr–smolt transformation. J. Fish. Res. Board Can. 27: 983–987.

KNUTSSON, S., AND T. GRAV. 1976. Seawater adaptations in Altantic salmon (*Salmo salar* L.) at different experimental temperatures and photoperiods. Aquaculture 8: 169–187.

KOMOURDJIAN, M. P., R. L. SAUNDERS, AND J. C. FENWICK. 1976a. Evidence for the role of growth hormone as a part of a 'light-pituitary axis' in growth and smoltification of Atlantic salmon (*Salmo salar*). Can. J. Zool. 54: 544–551.

1976b. The effect of porcine somatotropin on growth and survival in seawater of Atlantic salmon (*Salmo salar*) parr. Can. J. Zool. 54: 531–535.

MATHIASSON, M. 1970. Beneficial uses of heat in Iceland, p. 139–184. Proceedings of the Conference on Beneficial Uses of Thermal Discharges. N.Y. State Department of Environmental Conservation, Albany.

MCCARTNEY, T. H. 1976. Sodium–potassium dependent adenosine triphosphatase activity in gills and kidneys of Atlantic salmon (*Salmo salar*). Comp. Biochem. Physiol. 53A: 351–352.

PARRY, G. 1960. The development of salinity tolerance in the salmon *Salmo salar* (L.) and some related species. J. Exp. Biol. 37: 425–434.

PETERSON, H. H. 1973. Adult returns to date from hatchery reared one-year-old smolts. Int. Atl. Salmon Found. Spec. Publ. Ser. 4: 219–226.

PETERSON, H. H., O. T. CARLSON, AND S. JONASSON. 1972. The rearing of Atlantic salmon. Copyright Astra-Ewos, A. B. Sodertälje Sweden Bröd. Lgungberg Tryckeri A. B. Sodertälje,

Sweden. 39 p.

RITTER, J. A. 1972. Preliminary observation on the influence of smolt size on tag return rate and age at first maturity of Atlantic salmon *Salmo salar*. Int. Counc. Explor. Sea, C.M.1972/M:14. 10 p.

SAUNDERS, R. L. 1976. Heated effluent for the rearing of fry for farming and for release, p. 213–236. *In* O. Devih [ed.] Harvesting polluted waters. Plenum Publishing Corp., New York, NY.

SAUNDERS, R. L., AND E. B. HENDERSON. 1969. Survival and growth of Atlantic salmon parr in relation to salinity. Fish. Res. Board Can. Tech. Rep. 147. 14 p.

1970. Influence of photoperiod on smolt development and growth of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 27: 1295–1311.

1978. Changes in gill ATPase activity and smolt status of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 35: 1542–1546.

SUMARI, O., AND K. WESTMAN. 1980. Biological and economic aspects in the use of heated water for salmon smolt production as compared with traditional rearing. EIFAC/80/Symp:E/33.

TUUNAINEN, P., K. WESTMAN, O. SUMARI, AND E. VIRTANEN. 1980. Comparative rearing experiments with Baltic salmon (*Salmo salar*) fingerlings in heated brackish-water effluents and fresh water. EIFAC/80/Symp:E/46. 17 p.

VIRTANEN, E., K. WESTMAN, A. SOIVIO, AND P. TUUNAINEN. 1980. Physiological condition and smoltification of one-year-old Baltic salmon (*Salmo salar*) smolts reared in heated brackish-water effluents and fresh water. EIFAC/80/Symp:E/47.

WAGNER, H. H. 1974. Photoperiod and temperature regulation of smolting in steelhead trout (*Salmo gairdneri*). Can. J. Zool. 52: 219–234.

WAGNER, H. H., F. P. CONTE, AND J. L. FESSLER. 1969. Development of osmotic and ionic regulation in two races of chinook salmon (*Oncorhynchus tshawytscha*). Comp. Biochem. Physiol. 29: 325–341.

WEDEMEYER, G., R. L. SAUNDERS, AND W. C. CLARKE. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish Rev. 46: 1–14.

ZAUGG, W. S., B. L. ADAMS, AND L. R. MCLAIN. 1972. Steelhead migration potential temperature effects as indicated by gill adenosine triphosphotase activities. Science (Washington, D.C.) 176: 415–416.

ZAUGG, W. S., AND L. R. MCLAIN. 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (*Oncorhynchus kisutch*). Comp. Biochem. Physiol. 54A: 419–421.

ZAUGG, W. S., AND H. H. WAGNER. 1973. Gill ATPase activity to parr–smolt transformation and migration in steelhead trout. Influence of photoperiod and temperature. Comp. Biochem. Physiol. 45: 955–965.

A Procedure for Evaluating the Food Biomass Consumed by a Fish Population

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An application of the Ursin fish growth theory for evaluating the food biomass consumed by a fish population is proposed. In this procedure the total catabolism of a fish is treated as dependent on the level of available food. This is the major advantage of the procedure in comparison with that based on the most frequently used Winberg fish growth theory, in which the total catabolism rate is assumed to be independent of the available food level. The Atlantic cod (*Gadus morhua*) population inhabiting the southern Gulf of St. Lawrence (NAFO subarea 4T) in 1978 is considered in order to illustrate the procedure. The food biomass consumed by the cod population in this area and period is evaluated to be 0.727 million tonnes (the food consumption of the 0th cod age-group is not included). The uncertainty in the estimate of this food biomass due to uncertainties in the input parameters for the procedure is estimated to be in the range of 20% (standard error). Possible ways of improving the results of the procedure are discussed in the light of uncertainties in the input parameters and the sensitivity of the model upon them. It is concluded on the basis of a sensitivity analysis performed for the numerical example of procedure and the foraging theory for fish that the assumption introduced by Winberg can, in certain cases, introduce considerable bias to the procedure results.

Key words: fish, food consumption, growth, physiology, bioenergetics, cod, model, sensitivity analysis

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On propose dans l'article qui suit une application de la théorie d'Ursin sur la croissance des poissons dans l'évaluation de la biomasse alimentaire consommée par une population de poissons. Selon cette méthode, le catabolisme total d'un poisson est traité comme dépendant du niveau de nourriture disponible. C'est là le principal avantage de la méthode comparativement à celle utilisée le plus fréquemment, celle de Winberg, dans laquelle on suppose que le taux de catabolisme total est indépendant du niveau de nourriture disponible. Comme exemple, nous examinons la population de morues (*Gadus morhua*) du sud du golfe du Saint-Laurent (sous-zone 4T de l'OPANO) en 1978. On estime à 0,727 million de tonnes la biomasse de nourriture consommée par la population de morues dans cette région pendant cette période (ce chiffre n'inclut pas la quantité de nourriture consommée par les morues du groupe d'âge 0). On croit que le pourcentage d'erreur dans cette estimation de la biomasse alimentaire, résultant d'incertitudes dans les paramètres utilisés, se situe aux environs de 20 % (erreur type). Nous examinons diverses façons d'améliorer les résultats du procédé en fonction des incertitudes dans les paramètres d'entrée et de la sensibilité du modèle à leur endroit. En nous basant sur l'analyse de sensibilité effectuée dans l'exemple numérique de la méthode et sur la théorie de fourrage chez les poissons, nous en venons à la conclusion que l'hypothèse introduite par Winberg peut, dans certains cas, introduire un biais considérable dans les résultats de la méthode.

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KNOWLEDGE of the food biomass consumed by an animal population allows us to determine the influence of this population upon a lower trophic level. This consideration is related to several specific problems in the management of commercially important fish stocks. For example, information on interactions among predators and prey is required before conflicts related to exploitation of fish stocks from different trophic levels can be resolved (Gulland 1970). The estimates of food intake are also required for attempts to evaluate the instantaneous rates of predation mortality, frequently a major component of fish natural mortality (Mandecki 1976; Andersen and Ursin 1977; Majkowski 1977), within extended multispecies cohort analysis (Majkowski 1981a). The last approach aims to eliminate the uncertainty in the assessment of population abundance and age structure caused by uncertainties in the external estimates of natural mortality rates.

The feeding rates of fish in nature are very difficult to evaluate, although several methods have been employed (see review in Conover 1978; Mann 1978). Estimation of the food consumption rates based on turnover of gut contents has been performed for various species (e.g. Backiel 1971; Swenson and Smith 1973; Daan 1975; Elliott and Persson 1978). This method requires an accurate estimate of the gastric evacuation rate which is significantly affected by temperature (Kapoor et al. 1975), fish body size (Pandian 1967), meal size (Jobling et al. 1977; Beamish 1972), diet composition (Jones 1974; Elliott 1972), and sampling conditions (Eggers 1977).

An alternative approach for evaluating the food intake by a fish in nature is to simulate natural conditions in the laboratory and measure food consumption directly (e.g. Carline and Hall 1973). However, the direct methods prove to be difficult and tedious, and their attempts have seldom succeeded in simulating all required ranges of environmental variables (see discussion in Mann 1978). Thus, in practice the feeding rates in nature have been evaluated by directly extrapolating ration–growth data derived in the laboratory (e.g. Allen 1951; Horton 1961). Mann (1978) discusses the laboriousness of this approach and the frequent inadequacy of its assumptions for the situation in nature.

The third approach for estimating the food ration utilizes mathematical theories relating fish growth to food intake. Till now, the Winberg (1956) theory of fish bioenergetics is the one most often used for this purpose (see review in Conover 1978; Mann 1978). This theory can be treated as "a first approximation" to the fish growth process (see discussion in MacKinnon 1973; Conover 1978; and also Discussion section in this paper). To assure reliability of the food consumption estimates, a more advanced theory of fish growth should be used. Ursin (1967, 1979) introduced several important refinements to the Winberg theory (see Discussion section). This paper documents an attempt to utilize the Ursin fish growth theory for the purpose of food consumption evaluation. The Atlantic cod (*Gadus morhua*) population inhabiting the southern Gulf of St. Lawrence (NAFO subarea 4T) in 1978 is used to illustrate the procedure.

Outline of the Ursin Growth Theory

A full description of this theory and its empirical support has been presented elsewhere (Ursin 1967, 1979; Andersen and Ursin 1977); hence a brief description only is included here. The fish growth equation according to this theory is:

$$(1) \quad \frac{dw_i}{dt} = \beta_i(1 - \alpha_i)\frac{dR_i}{dt} - k_i w_i^{n_i} - e_i(t,w_i)$$

where w_i is the body weight (g), t is time (yr), dR_i/dt is the instantaneous rate of food consumption (g/yr), β_i is the assimilated fraction of food eaten by a fish, k_i is the coefficient (temperature dependent) of the term for fasting (i.e. during starvation) catabolism (g^{1-n_i}/yr), n_i is the power value of the term for fasting catabolism, α_i is the fraction of assimilated food lost in feeding catabolism (i.e. total catabolism reduced by fasting catabolism), and e_i is the instantaneous rate of spawning (g/yr). Subscript i identifies constants and variables with respect to age-group and calendar year. The ith age-group consists of fish which become i yr old in the calendar year under consideration. The above equation can be presented in the form:

$$(2) \quad \frac{dw_i}{dt} = \beta_i(1 - \alpha_i)\frac{dR_i'}{dt} - k_i w_i^{n_i}$$

where

$$(3) \quad \frac{dR_i'}{dt} = \frac{dR_i}{dt} - \frac{e_i(t,w)}{\beta_i(1 - \alpha_i)}.$$

The rate dR_i'/dt can be interpreted as the consumption rate of food utilized for somatic growth and maintenance expenses. It has been demonstrated for various animal species that the instantaneous rate of food consumption can be approximated by a power function of the animal's body weight. This is particularly valid in the case of fish, for which Ursin (1967, 1979) proposed the following relationship:

$$(4) \quad \frac{dR_i}{dt} = \hat{H}_i w_i^{m_i}$$

where the parameter $\hat{H}_i$ (g^{1-m_i}/yr) is implicitly dependent on the level of available food for a fish and temperature, i.e. $\hat{H}_i$ can change its value from year to year (Ursin 1967, 1979). Because the rate $[e_i(t,w_i)/\beta_i(1 - \alpha_i)]$ is frequently much smaller than dR_i/dt (see Example of Application section), it can be assumed that the consumption rate of food utilized for somatic growth is also a power function of the fish body weight. Hence

$$(5) \quad \frac{dR_i'}{dt} = \hat{H}_i' w_i^{m_i}$$

where the parameter $\hat{H}_i'$ (g^{1-m_i}/yr) is implicitly dependent on the level of available food and temperature.

Outline of the Procedure

As outlined above, the Ursin growth equation relates fish growth to food consumption. Thus, the food biomass consumed by a fish population can be estimated if the required physiological parameters (i.e. α_i, β_i, m_i, n_i, and k_i), growth

data, and the number of fish within each age-group are known. The simplest way to estimate the parameter values for the Ursin growth theory is to fit equations (2) and (5) to the empirical growth data. However, these equations contain a number of parameters, and the resultant evaluation can lead to parameter values which generate curves which approximate well the empirical growth data, but do not correspond to their biological interpretation. Therefore, the parameters claimed to be strongly independent of the actual feeding rate (i.e. α_i, β_i, m_i, n_i, and k_i, see Ursin 1967, 1979; Andersen and Ursin 1977; and Discussion section of this paper) should be determined on the basis of laboratory studies (for methods see Ursin 1967, 1979; Andersen and Ursin 1977; Sperber et al. 1977) whereas $\dot{H}_i$ should be found by fitting the solution of differential equations (2) and (5) to the empirical fish growth data (see Example of Application section). The calculated values of $\dot{H}_i$ can change from year to year as equations (2) and (5) incorporate the dependence of the fish growth rate on (i) the food intake (resultant from the actual food availability and temperature) and (ii) the catabolism rate influenced by the food intake, temperature, and the growth data reflecting the actual food availability and temperature.

The yearly average consumption of food utilized for somatic growth can be estimated on the basis of equation (5) using the calculated values of $\dot{H}_i$ and the yearly average body weights of fish within each age-group. Then, the yearly total food consumption can be calculated as the sum of the yearly consumption of food utilized for somatic growth and maintenance expenses, and the value of $[e_i(t,w)/\beta_i(1-\alpha_i)]$ cumulated over the year. The average numbers of fish within each age-group are additionally required to estimate the yearly food biomass consumed by the population.

Example of Application

The Atlantic cod (*G. morhua*) population inhabiting the southern Gulf of St. Lawrence in 1978 is considered to illustrate this procedure.

Determination of Input Parameter Values

The assimilated fraction of food eaten by a cod, β_i, and the fraction of assimilated food lost in feeding catabolism, α_i, are assumed to be independent of cod size, actual feeding rate, temperature, and equal to 0.8 and 0.4, respectively (see Winberg 1956; Ursin 1967, 1979; Andersen and Ursin 1977; Discussion section). The values of the powers m_i and n_i are estimated on the basis of laboratory studies (cf. Andersen and Ursin 1977) as equal to 0.56 and 0.83, respectively.

The coefficient of the term for fasting catabolism, k_i, is evaluated on the basis of laboratory experiments carried out by Kohler (1964) concerning the so-called maintenance food ration for a cod under similar environmental conditions (temperature) as those in the southern Gulf of St. Lawrence. According to equation (1) the yearly maintenance food ration, $dR_i/dt_{\text{main.}}$, should satisfy the following condition:

$$(6) \quad \beta(1-\alpha)\frac{dR_i}{dt_{\text{main.}}} - k_i w^n = 0.$$

The yearly maintenance food ration is determined by Kohler (1964) as equal to 1176 and 1375 g/yr for 513- and 751-g cod, respectively. Utilizing equation (6), Kohler's observations, and the values of parameters determined above, k_i is calculated to be equal to 3.18 and 2.70, for the smaller and larger cod, respectively. Because k_i should be independent of cod age (Ursin 1967, 1979; Andersen and Ursin 1977), the mean value of k equal to 2.94 is used in further calculations.

The values of $\dot{H}_i$ are estimated by fitting the solution of differential equations (2) and (5) to the empirical cod growth data (see Appendix). The finite-difference Leverberg–Marquardt algorithm (Marquardt 1963; Brown and Dennis 1972) is used to fit the solution of differential equations (2) and (5) to the growth data. Equations (2) and (5) are solved with the aid of the Runge–Kutta–Verner method of the fifth order (Hull et al. 1976). Table 1 displays the calculated values of $\dot{H}_i$. Because it was impossible to find the value $\dot{H}_i$ for the 12th, 14th, and 15th age-groups (see Table 1), it is assumed that $\dot{H}_{12}$ is equal to $\dot{H}_{11}$; similarly, $\dot{H}_{14}$ and $\dot{H}_{15}$ are assumed to be equal to $\dot{H}_{13}$.

Bagenal (1973, 1978) has shown that the fecundity of a fish increases with its body size according to the allometric law. Thus, the biomass of reproductive products spawned during the year by an average mature cod belonging to the ith age-group, E_{mi}, can be treated as:

$$(7) \quad E_{mi} = aw_i^b$$

where a and b are positive constants. Ware (1980) evaluates the values of a and b for cod on the basis of Powles' (1958) data for the southern Gulf of St. Lawrence as equal to 0.0026 and 1.38, respectively. These estimates lead to the yearly values of reproductive products which seem to be underestimated (for instance, for a 7000-g cod E_{mi} appears to be equal to 7.5% of its body weight whereas E_{mi} is claimed (Parrish 1975) to average 10% of the cod body weight). Therefore, the value of a is adjusted to be consistent with the last evaluation. Tentatively, it is assumed that the average yearly value of reproductive products for a large cod (e.g. 7000 g) is about 15% of its weight. This condition leads to the value of a equal to 0.0052. Under the above assumptions, the yearly value of reproductive products for a small mature cod is calculated to be less than 10% of its weight whereas for a large mature cod is greater than 10%; as will be shown later (see Sensitivity Analysis section), accurate estimation of a is not important from the viewpoint of the present study.

The biomass of reproductive products spawned during the year by an average cod of the ith age-group can be determined on the basis of the following formula:

$$(8) \quad E_i = \frac{p_i}{100\%} E_{mi}$$

where E_{mi} is estimated on the basis of formula (7) and p_i is the percent of mature cod within the ith age-group in 1978, evaluated as 0% for the 1st and 2nd age-groups, 31 and 81% for the 3rd and 4th age-groups, respectively, and 100% for the older age-groups (the data provided by Dr T. D. Beacham).

The average number of cod ($\bar{N}_i$) within the ith age-group during 1978 can be calculated as follows (see Ricker 1975):

TABLE. 1. Values of cod physiological parameters for 1978 (for explanation of symbols see the Example of Application section or Glossary).

	Age-group[a]														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$\bar{w}_i$ (g)	100	200	380	680	1040	1670	2260	2780	4050	4320	5850	5540	6260	5040	7000
$\dot{H}_i$ ($g^{0.44}$/yr)	40.72	40.72	49.26	52.72	55.92	58.72	59.42	57.55	64.30	59.23	73.45	—[b]	70.36	—[b]	—[b]
ΔR_i (g/yr)	537	791	1371	2033	2736	3746	4495	4883	6736	6432	9454	9170	9406	8331	10014
E_i (g)	0	0	6	34	76	146	221	294	495	541	822	762	902	669	1053
ΔR_{E_i} (g/yr)	0	0	12	71	158	303	461	613	1031	1126	1712	1588	1879	1394	2193
ΔR_i (g/yr)	537	791	1384	2104	2894	4049	4956	5497	7766	7559	11166	10758	11286	9724	12206
$\Delta C_{\text{fast},i}$ (g/yr)	135	239	407	661	940	1392	1790	2125	2905	3064	3941	3767	4169	3483	4574
ΔC_i (g/yr)	306	492	850	1334	1866	2688	3376	3884	5390	5483	7514	7210	7781	6595	8480
ΔP_i (g/yr)	123	141	257	350	449	551	589	513	823	564	1418	1397	1248	1185	1285
K_{1i}	0.23	0.18	0.19	0.17	0.16	0.14	0.12	0.09	0.11	0.7	0.13	0.13	0.11	0.12	0.11
ΔR_{m_i} (g)	93	166	283	458	652	966	1242	1475	2015	2126	2734	2613	2892	2416	3173
ΔR_{4T_i} (g)	443	625	1101	1646	2242	3083	3714	4022	5751	5433	8432	8145	8393	7308	9033

[a]The ith age-group consists of fish becoming i yr old in 1978.
[b]No value is estimated because the empirical growth data are evidently inconsistent for this age-group (see Appendix).

$$(9) \quad \bar{N}_i = \frac{N_{0i}(1 - e^{-Z_i})}{Z_i}$$

where N_{0i} is the number of cod within the ith age-group at the beginning of the year 1978 (Fig. 1, Appendix) and Z_i is the instantaneous rate of total mortality for the ith age-group ($Z_i = F_i + M_i$, where F_i and M_i are the instantaneous rates of fishing and natural mortality, respectively; $M_i = 0.2$ according to Gray (1979) and the values of F_i are presented in the Appendix).

RESULTS

The yearly consumption of food utilized for somatic growth and maintenance expenses, ΔR_i (estimated on the basis of equation (5), the values of $\dot{H}_i$, and the average body weights of cod within each age-group during 1978, $\bar{w}_i$, assumed to be equal to the body weights in June 1978, see Appendix) is presented in Table 1. The total yearly food consumption, ΔR_i, is calculated by adding the yearly consumption of food utilized for reproduction and associated expenses,

$$(10) \quad \Delta R_{E_i} = \frac{1}{\beta(1 - \alpha)} \int_0^1 e_i(t, w_i(t))dt = \frac{E_i}{\beta(1 - \alpha)}$$

(see Table 1).

The yearly food assimilation can be calculated within the model as a constant fraction ($\beta = 0.8$) of ΔR_i (Winberg 1956; Ursin 1967, 1979; Andersen and Ursin 1977).

According to the Ursin model the yearly catabolism, ΔC_i, can be evaluated as a sum of the yearly fasting catabolism, $\Delta C_{\text{fast},i}$ ($\Delta C_{\text{fast},i} = k\bar{w}_i^n$), and the yearly feeding catabolism, $\Delta C_{\text{feed},i}$ ($\Delta C_{\text{feed},i} = \alpha\beta\Delta R_i$). The results (see Table 1) show that the rate of total catabolism is about two times higher than that of fasting catabolism. This agrees with Winberg's (1956; see also Kerr 1971a, b, c; Ware 1975; Mann 1978) bioenergetic generalizations regarding fish living in the natural environment.

The yearly total production, ΔP_i, can be evaluated on the basis of the following equation:

$$(11) \quad \Delta P_i = \beta(1 - \alpha)\Delta R_i - k\bar{w}_i^n$$

(see Table 1). Utilizing the values of ΔP_i and ΔR_i, the instantaneous coefficient of utilization of consumed food for total production, K_{1i}, can be calculated:

$$(12) \quad K_{1i} = \frac{\Delta P_i}{\Delta R_i}$$

(see Table 1). The coefficient tends to be a decreasing function of cod age. This agrees well with the general knowledge on fish bioenergetics (Parker and Larkin 1959; Jones and Hislop 1978). The range of values for K_{1i} is consistent with that expected for fish living in natural conditions.

Because the cod population leaves area 4T for about 4 mo from January to May (McKenzie 1956; McCracken 1959; Martin and Jean 1964) during which the cod weights are approximately constant (Lett 1978), the biomass of food consumed by a cod during these 4 mo, ΔR_{Vn_i}, is estimated (see

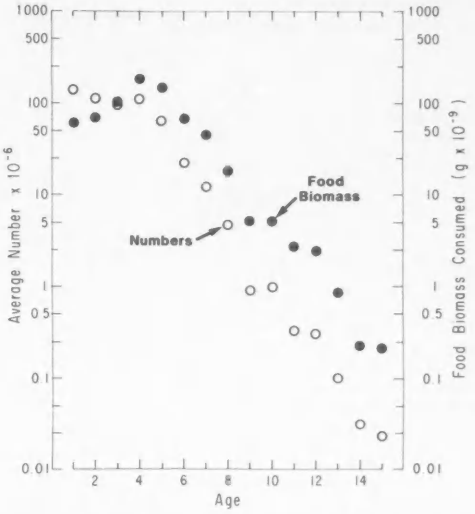

FIG. 1. Yearly average number ($\bar{N}_i$) of cod within the ith age-group and the food biomass consumed during 1978 by the ith cod age-group in the southern Gulf of St. Lawrence ($\bar{N}_i \times \Delta R_{4Ti}$) as functions of i. (To obtain the actual values one must multiply the numbers on the Y-axes by 10^6 for cod numbers and 10^9 for food biomass consumed.)

Table 1) to be equal to one-third of its yearly maintenance ration (see equation (6)). Finally, the biomass of food consumed by a cod in area 4T, R_{4Ti}, is calculated as a difference between ΔR_i and ΔR_{Vn_i} (see Table 1).

The food biomass consumed by each cod age-group in the southern Gulf of St. Lawrence during 1978 is calculated (Fig. 1) as a product of ΔR_{4Ti} and $\bar{N}_i$. The total food biomass consumed by the cod population in area 4T during 1978 is evaluated to be equal to 0.727 million tonnes. The estimate does not include the food biomass consumed by the 0th cod age-group.

SENSITIVITY ANALYSIS

Method — Identification of input parameters to which the output of a procedure is most sensitive leads not only to a better understanding of this procedure but also eliminates unnecessary empirical and theoretical investigations concerning noncritical parameters. An effective approach to this identification is sensitivity analysis (e.g. Tomovic 1963; Kowal 1971; Miller 1974; Miller et al. 1976; Waide and Webster 1976; Majkowski and Bramall 1980; Majkowski et al. 1980, 1981; Majkowski 1981b). Ordinary sensitivity analysis (dealing with nonsimultaneous changes in input parameters) can provide information about the performance of the procedure when its input parameters are slightly changed indicating parameters which, if changed, produce either strong or weak changes in the output (for details see Majkowski and Bramall 1980).

Examination of the procedure developed in this paper is initiated by ordinary sensitivity analysis. One after another, the value of each input parameter is increased and decreased by various fixed percentages (for convenience of presenting the results some parameter values are simultaneously changed, see Table 2). The effects of such perturbations on the procedure performance are determined by analyzing the relative changes in the total food biomass consumed by the cod population in area 4T during 1978. This last value will be referred to as D-measure in the traditional sense (see Miller 1974; Miller et al. 1976; Majkowski and Bramall 1980; Majkowski et al. 1981; Majkowski 1981b). It is emphasized that a change in α, β, or n causes a change in the estimate of k (see Determination of Parameter Values section). Similarly, a change in α, β, m, n, k, or growth data affects the estimates of $\hat{H}_i$. This is taken into account in the sensitivity analysis.

Recently, a few extensions to the ordinary sensitivity analysis have been developed for determination of the output uncertainty due to uncertainties in input parameters (see Miller 1974; Miller et al. 1976; Majkowski et al. 1981; Majkowski 1981b). Under the assumption that errors in input parameters have normal distributions, are not cross-correlated, and a linear theory associated with the additive sensitivity analysis is valid, the variance in the D-measure can be estimated on the basis of the following formula (Miller 1974; Miller et al. 1976; Majkowski 1981b):

$$\text{(13)} \quad \text{var}(D) = \sum_{j=1}^{67} R_j^2 \text{var}(u_j)$$

where summation in the above formula is performed over all input parameters, $\text{var}(u_j)$ is the variance of u_j (u_j is the relative error in the jth input parameter) and

$$\text{(14)} \quad R_j = \frac{\partial D}{\partial u_j}.^2$$

To estimate $\text{var}(D)$, the variances of u_j have to be specified (see Table 3) and the values of R_j have to be numerically determined (see Table 4).

Results — Several facts are evident from the results of ordinary sensitivity analysis (see Table 2): (i) For the majority of input parameters (i.e. excluding b, n, and β) the D-measure (see Method section) can be treated as a linear function of u for values of u in the range up to tens of percentages. (ii) The D-measure is very sensitive to changes in (listed in order of importance): w_i (June 1978), $\bar{N}_i$, k, β, α, w_i (Jan. 1977), b, and m. (iii) The D-measure is insensitive to changes in p_i, a, and n.

The contributions of input parameter uncertainties to the variance of D, under the assumptions specified in the Method section, are displayed in Table 4. The total variance of D is equal to 0.038. This means that the standard deviation for the calculated food biomass consumed by the cod population in area 4T during 1978 is in the range of 20%. Such an output uncertainty seems to be quite acceptable.

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[2]The value of $\partial D/\partial u_j$ is traditionally denoted by R_j (see Miller 1974; Miller et al. 1976; Majkowski 1981b). There is no conjunction between R_j from formula (14) and dR_i/dt from previous sections. Convergence of the symbols is incidental.

TABLE. 2. Results of ordinary sensitivity analysis.

Perturbed parameter	Perturbation magnitude			
	−25%	−1%	+1%	+25%
	Relative change (expressed in percentage) in the food biomass consumed during 1978 by the cod population in area 4T			
$\underline{w}_i$ (June 1978)[a]	30.42	1.24	1.24	−31.33
$\overline{N}_i$[a]	25.00	1.00	−1.00	−25.00
k	12.57	0.51	−0.51	−12.75
β	−16.57	−0.50	0.49	9.80
α	7.02	0.33	−0.33	−9.92
w_i (Jan. 1977)[a]	−8.10	−0.30	0.30	7.06
b	4.86	0.52	−0.56	−60.49
m	4.03	0.21	−0.21	−6.52
n	−4.10	−0.09	0.08	0.66
a	1.33	0.05	−0.05	−1.33
p_i[a]	1.32	0.05	−0.05	−1.33

[a]All values (i.e. for $i = 1, 2, 3, \ldots, 15$) are simultaneously perturbed by the same percentage indicated in the first row.

TABLE. 3. Errors specification for input parameters.

	Parameter										
	w_i (June 1978)	$\overline{N}_i$	k	β	α	w_i (Jan. 1978)	b	m	n	a	p_i
Standard deviation[a] (in %)	15[b]	30[c]	15	10	20	15	10	15	10	25	15

[a]Estimated on the basis of available scientific literature and in consultation with experts.

[b]Standard deviation can be higher for first and last few age-groups because of partial recruitment of the first few age-groups to the fishery and because of small numbers of samples for the last few age-groups.

[c]Usually, higher uncertainties are associated with the numbers-at-age. These numbers are derived within the cohort analysis (Gray 1979) claimed by the Canadian Atlantic Scientific Advisory Committee to be exceptionally reliable.

The uncertainties in the following input parameters: $\overline{N}_i$, w_i (June 1978), k, α, b, and β contribute about 38, 16, 15, 12, 8, and 6%, respectively, to the total variance of D. The uncertainties in the other input parameters (i.e. p_i, n, a, w_i (Jan. 1977), and m) participate insignificantly to the total variance of D (about 5%).

It should be emphasized that not all conclusions derived from the present analysis have to be strictly valid for other fish populations for which we can expect different parameter values and their error ranges.

Discussion

The presented example shows the usefulness of the proposed procedure for evaluating the food biomass consumed by a fish population. The total catabolism of a fish is treated within this procedure as dependent on the food intake resultant from the food availability. This is the major advantage of this procedure in comparison with that based on the Winberg (1956) fish growth theory, within which the total catabolism rate is assumed to be independent of the available food level. In light of the sensitivity analysis it is concluded that the last assumption can introduce, in certain cases, considerable bias to the procedure results. The strong dependence of the procedure results on the value of α infers that the variability in the total catabolism rate strongly influences the procedure output. The foraging theory for fish provides evidence, independent of the Ursin growth theory, that the total catabolism rate is strongly conditioned in nature by the level of available food (Ware 1975, 1978). According to this theory, forage-related swimming activities increase with the level of available food. This conclusion is confirmed by the study carried out by Kerr (1971a). Also, that portion of the total catabolism which is contributed by specific dynamic action (SDA) increases proportionally to the food consumption (Yahl and Davenport 1979). The increase in the total catabolism with an increase in the level of available food was observed for cod by Edwards et al. (1972). Thus, it can be expected that the procedure for evaluating the food consumption based on the Winberg fish growth theory is not universally valid. This is already empirically confirmed; the procedure provides reasonable results only for specific feeding conditions (see review in Conover 1978).

The parameters α_i, β_i, m_i, n_i, and k_i are assumed in the procedure (see Outline of the Procedure section) to be independent of the actual feeding rate. Because n_i and k_i are responsible for the catabolism rate during starvation, they obviously cannot be dependent on the food intake rate. The value of α is not likely to be dependent on the feeding rate. The relation of β to the food consumption rate possibly takes

TABLE. 4. Relative sensitivity coefficients ($R_{par.}$) and contributions ($R^2_{par.} \times \text{var}(u_{par.})$) of input parameter uncertainties to the variance of D (only the values associated with the parameters contributing significantly to the variance of D are presented; all numbers are rounded).

	Age-group															$\sum_i$
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
$R_{\overline{N}_i}$	−0.0869	−0.1003	−0.1439	−0.2560	−0.2022	−0.0971	0.0637	−0.0261	−0.0074	−0.0074	−0.0038	−0.0034	−0.0012	0.0003	0.003	
$R^2_{\overline{N}_i} \times \text{var}(u^2_{\overline{N}_i})$	0.0007	0.0009	0.0019	0.0059	0.0037	0.0008	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000	0.0143
$R_{w_i(\text{June } 1978)}$	−0.0436	−0.0489	−0.2390	−0.3126	−0.2657	−0.1406	−0.0996	−0.0445	−0.0129	−0.0140	−0.0104	−0.0021	−0.0029	0.0002	0.0002	
$R^2_{w_i(\text{June } 1978)} \times \text{var}(u_{w_i})$	0.000	0.001	0.0013	0.0022	0.0016	0.0004	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0059
R_k	−0.5066															
$R^2_k \times \text{var}(u_k)$	0.0058															0.0058
R_α	−0.3313															
$R^2_\alpha \times \text{var}(u_\alpha)$	0.0044															0.0044
R_β	0.5570															
$R^2_\beta \times \text{var}(u_\beta)$	0.0031															0.0031
R_β	0.4886															
$R^2_\beta \times \text{var}(u_\beta)$	0.0024															0.0024

the form of one of the formulas derived by Ursin (1967, 1979), Elliot (1976b), or Sperber et al. (1977). The dependence of α_i and β_i on the food intake rate, if explicitly known, can be accounted for in the procedure. The dependence of m_i on the feeding rate, which is unlikely to be present and is unimportant in the light of sensitivity analysis, cannot be included in the procedure.

The results of the performed sensitivity analysis allow us to make some recommendations for further studies. They indicate that reliable estimates for the numbers-at-age of fish and the accurate growth data are required. The parameter k is dependent on temperature (see Ursin 1967, 1979) and, therefore, can change its value from year to year. In the example considered this relationship should be given greater weight than it has received here. (A possible form of this relationship can be found in Kitchell et al. (1977), Ursin (1967, 1977), Stewart (1980), or Kitchell and Breck (1980).) It is claimed (cf. Ursin 1967, 1979; Andersen and Ursin 1977) that α and β are not strongly dependent on temperature (the relations of α and β to temperature possibly take the form of those derived by Ursin (1967) and Elliott (1976a), respectively) and cod body size; nevertheless, this should be further examined and the present values verified. Because these two parameter values are possibly dependent on prey type, they should be determined for, at least, major prey items. This would permit adjustment in the procedure for compositional changes in the diet. If possible, the values of a and b should be estimated for a particular year and area under consideration. The results of the performed analysis suggest that the accurate estimates for p_i, n, a, and m are not particularly important for the present application of the Ursin model.

The use of energy units rather than wet mass units seems to be more appropriate for the majority of implementation purposes of the Ursin growth theory. The present calculations are performed in wet mass units as appropriate energy equivalents for the area and year under consideration were not available. Wet mass units are also used by Ursin (1967, 1979; Andersen and Ursin 1977). Although the studies carried out by Daan (1975) for the cod population inhabiting the North Sea indicate that the energy equivalents for cod body weight, reproductive products, and food (average natural composition) for that area are very similar (differences in the range of 10%), it should be emphasized that the cod diet composition can strongly change from year to year and the energy equivalents for various cod prey do differ (Daan 1975).

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ALLEN, K. R. 1951. The Horokiwi Stream: a study of a trout population. Fish. Bull. N.Z. 10: 1–238.

ANDERSEN, K. P., AND URSIN, E. 1977. A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. Medd. Dan. Fisk. Havunders. N.S. 7: 319–435.

BACKIEL, T. 1971. Production and food consumption of predatory fish in the Vistula River. J. Fish. Biol. 3: 369–405.

BAGENAL, T. B. 1973. Fish fecundity and its relations with stock and recruitment. Rapp. P. V. Reun. Cons. Int. Explor. Mer 25: 73–80.

1978. Aspects of fish fecundity, p. 75–101. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. John Wiley & Sons, New York and Toronto.

BEAMISH, F. W. H. 1972. Ration size and digestion in large mouth bass, *Micropterus salmoides* Lacepede. Can. J. Zool. 50: 153–164.

BROWN, K. M., AND J. E. DENNIS. 1972. Derivative free analogues of the Levenberg-Marquardt and Gauss algorithms for nonlinear least squares approximations. Num. Math. 18: 289–297.

CARLINE, R. F., AND J. D. HALL. 1973. Evaluation of a method for estimating food consumption rates of fish. J. Fish. Res. Board Can. 30: 623–629.

CONOVER, R. J. 1978. Transformation of organic matter, p. 221–489. *In* O. Kinne [ed.] Marine ecology. Vol. IV — Dynamics. John Wiley & Sons, New York and Toronto.

DAAN, N. 1975. Consumption and production in North Sea cod *Gadus morhua*: an assessment of the ecological status of the stock. Neth. J. Sea Res. 3: 24–55.

EDWARDS, R. R. C., D. M. FINLAYSON, AND J. H. STEELE. 1972. An experimental study of the oxygen consumption, growth and metabolism of the cod (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. 8: 299–309.

ELLIOTT, J. M. 1972. Rates of gastric evaluation in brown trout (*Salmo trutta* L.). Freshwater Biol. 2: 1–18.

1976a. Energy losses in the waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. 45: 561–580.

1976b. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. 45: 923–948.

ELLIOTT, J. M., AND L. PERSSON. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977–991.

EGGERS, D. M. 1977. Factors in interpreting data obtained by diet sampling of fish stomachs. J. Fish. Res. Board Can. 34: 290–294.

GRAY, D. 1979. 1979 Assessment of cod in Division 4T and 4Vn (Jan.–Apr.). Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 79/21. 28 p.

GULLAND, J. A. 1970. Food chain studies and some problems in world fisheries, p. 296–315. *In* J. H. Steele [ed.] Marine food chains. Oliver and Boyd, Edinburgh.

HORTON, P. A. 1961. The bionomics of brown trout in a Dartmoor stream. J. Anim. Ecol. 30: 311–338.

HULL, T. E., W. H. ENRIGH, AND K. R. JACKSON. 1976. User's guide for DVERK a subroutine for solving non-stiff ODE's. Univ. Toronto, Department of Computer Science, Technical Report No. 100.

JOBLING, J., D. GWYTHER, AND D. J. GROVE. 1977. Some effects of temperature, meal size, and body weight on gastric evacuation of the dab *Limanda limanda* (L.). J. Fish Biol. 10: 291–298.

JONES, R. 1974. The rate of elimination of food from the stomachs of haddock, *Metanogrammus aegleinnus*, cod, *Gadus morhua* and whiting, *Merlangius merlangus*. J. Cons. Cons. Int. Explor. Mer 35: 225–243.

JONES, R., AND J. R. G. HISLOP. 1978. Further observations on the relation between food intake and growth of gadoids in captivity. J. Cons. Cons. Int. Explor. Mer 38: 244–251.

KAPOOR, B. G., H. SMITZ, AND I. A. VERIGHINA. 1975. The alimentary canal and digestion in teleosts. Adv. Mar. Biol. 13: 109–239.

KERR, S. R. 1971a. Analysis of laboratory experiments on growth efficiency of fishes. J. Fish. Res. Board Can. 28: 801–909.

1971b. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. 28: 809–814.

1971c. A simulation model of lake trout growth. J. Fish. Res. Board Can. 28: 815–819.

KITCHELL, J. F., AND J. E. BRECK. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2159–2168.

KITCHELL, J. F., D. J. STEWART, AND D. WEININGER. 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*) J. Fish. Res. Board Can. 34: 1922–1935.

KOHLER, A. C. 1964. Variations in the growth of Atlantic cod (*Gadus morhua* L.). J. Fish. Res. Board Can. 21: 57–100.

KOWAL, N. E. 1971. A rationale for modelling dynamic ecological systems, p. 123–192. *In* B. C. Patten [ed.] Systems analysis and simulation in ecology. Vol. 1. Academic Press, New York, NY.

LETT, P. F. 1978. A comparative study on the recruitment mechanisms of cod, and mackerel, their interaction, and its implication for dual stock management. Ph.D. dissertation, Dalhousie Univ., Halifax, N.S. 125 p.

MACKINNON, J. C. 1973. Analysis of energy flow and production in an unexploited marine flatfish population. J. Fish. Res. Board Can. 30: 1717–1728.

MAJKOWSKI, J. 1977. Prognosis for catches of cod, herring and sprat in the Baltic Sea and their optimization with the aid of a mathemetical model. Pol. Arch. Hydrobiol. 24: 361–382.

1981a. Application of a multispecies approach for assessing the population abundance and the age-structure of fish stocks. Can. J. Fish. Aquat. Sci. 38: 424–431.

1981b. Usefulness and applicability of sensitivity analysis in a multi-species approach to fisheries management. Proceedings of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multi-Species Stocks (12–24 January 1981, Cronulla, NSW, Australia). (In press)

MAJKOWSKI, J., AND L. BRAMALL. 1980. Sensitivity of bioenergetic growth models of animals to changes in the energy balance parameters. J. Theor. Biol. 85: 643–655.

MAJKOWSKI, J., J. PILARSKA, AND R. Z. KLEKOWSKI. 1980. Simulations of energy flow through the amictic female rotifer *Brachionus rubens* Ehrbg. Can. J. Fish. Aquat. Sci. 37: 97–110.

MAJKOWSKI, J., J. R. RIDGEWAY, AND D. R. MILLER. 1981. Multiplicative sensitivity analysis and its role in development of simulation models. Ecol. Model. 12: 191–208.

MANDECKI, W. 1976. A computer simulation model for interacting fish population studies, applied to the Baltic. Pol. Arch. Hydrobiol. 23: 281–307.

MANN, K. H. 1978. Estimating the food consumption of fish in nature, p. 250–273. *In* S. G. Gerking [ed.] Ecology of freshwater fish production. John Wiley & Sons, New York and Toronto.

MARQUARDT, D. W. 1963. An algorithm for least-squares estimation of nonlinear parameters. J. Ind. Appl. Math. 11: 431–441.

MARTIN, W. R., AND Y. JEAN. 1964. Winter cod taggings off Cape Breton and offshore Nova Scotia banks 1959–62. J. Fish. Res. Board Can. 21: 215–238.

MCCRACKEN, F. D. 1959. Cod tagging off northern New Brunswick in 1955 and 1956. Fish. Res. Board Can. Prog. Rep. Atl. Coast Stn. 72: 8–19.

MCKENZIE, R. A. 1956. Atlantic cod tagging off the southern Canadian mainland. Bull. Fish. Res. Board Can. 105:1–93.

MILLER, D. R. 1974. Sensitivity analysis and validation of simulation

models. J. Theor. Biol. 48: 345–360.

MILLER, D. R., G. BUTTLER, AND L. BRAMALL. 1976. Validation of ecological system models. J. Environ. Manage. 4: 383–401.

PANDIAN, T. J. 1967. Intake, digestion, absorption and conversion of food in the fish, *Megalops cyprinoides* and *Ophiocephalus striatus*. Mar. Biol. 1: 16–32.

PARRISH, J. D. 1975. Marine trophic interactions by dynamic simulation of fish species. U.S. Fish Wildl. Fish. Bull. 73: 695–717.

PARKER, R. R., AND P. A. LARKIN. 1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16: 721–745.

POWLES, P. M. 1958. Studies on reproduction and feeding of Atlantic cod (*Gadus callanies* L.) in the Southern Gulf of St. Lawrence. J. Fish. Res. Board Can. 15: 1383–1402.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191.

SPERBER, O., J. FROM, AND P. SPARRE. 1977. A method to estimate the growth rate of fishes, as a function of temperature and feeding level, applied to rainbow trout. Medd. Dan. Fisk. Havunders. N.S. 7: 275–317.

STEWART, D. J. 1980. Salmoid predators and their forage base in Lake Michigan: a bioenergetics-modelling synthesis. Ph.D. thesis, Univ. Wisconsin, Madison. 225 p.

SWENSON, W. A., AND L. L. SMITH JR. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye *Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 32: 33–41.

TOMOVIC, R. 1963. Sensitivity analysis of dynamic systems. McGraw-Hill Book Company Inc., New York. 142 p.

URSIN, E. 1967. A mathematical model of some aspects of fish growth, respiration and mortality. J. Fish. Res. Board Can. 24: 2355–2453.

1979. Principles of growth in fishes. Symp. Zool. Soc. London 44: 63–87.

WAIDE, J. B., AND J. R. WEBSTER. 1976. Engineering systems and analysis: applicability to ecosystems, p. 330–372. *In* B. C. Patten [ed.] System analysis and simulation in ecology. Vol. IV. Academic Press, New York, NY.

WARE, D. M. 1975. Growth, metabolism and optimal swimming speed of a pelagic fish. J. Fish. Res. Board Can. 32: 33–41.

1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. J. Fish. Res. Board Can. 35: 220–228.

1980. Bioenergetics of stock and recuitment. Can. J. Fish. Aquat. Sci. 37: 1012–1024.

WINBERG, G. G. 1956. Rate of metabolism and food requirements of fish. Nauchn. Tr. Belorusskogo Gos. Univ. Imni V. I. Lenina, Minsk. 253 p. (Fish. Res. Board Can. Transl. Ser. No. 194. 202 p.)

YAHL, O., AND J. DAVENPORT. 1979. Apparent specific dynamic action of food in the fish *Blennius pholis*. Mar. Ecol. Prog. Ser. 1: 109–113.

Glossary

a	Coefficient of the formula relating the biomass of reproductive products spawned by a cod during the year to its body weight (g^{1-b})
b	Power value of the formula relating the biomass of reproductive products spawned by a cod during the year to its body weight (dimensionless)
$\frac{dR_i}{dt}$	Instantaneous rate of food consumption (g/yr)
$\frac{dR_i'}{dt}$	Instantaneous consumption rate of food utilized for somatic growth and maintenance expenses (g/yr)
$\frac{dR_i}{dt_{\text{main.}}}$	Yearly maintenance food ration (g/yr)
D	D-measure ($D = B^0 - B)/B^0$, where B^0 and B are the estimates of the food biomass consumed by the cod population in area 4T during 1978 for unperturbed and perturbed input parameters, respectively (dimensionless)
e_i	Instantaneous rate of spawning (g/yr)
E_i	Biomass of reproductive products spawned during 1978 by an average cod (g)
E_{mi}	Biomass of reproductive products spawned during 1978 by an average mature cod (g)
F_i	Instantaneous rate of fishing mortality (yr^{-1})
$\hat{H}_i$	Coefficient of the formula relating the total food consumption rate to the body weight (g^{1-m_i}/yr)
$\hat{H}_i'$	Coefficient of the formula relating the consumption rate of food utilized for somatic growth to the body weight (g^{1-m_i}/yr)
i	Index denoting age-groups (the ith age-group consists of fish becoming i yr old in the calendar year under consideration) (dimensionless)
j	Index denoting input parameters for the procedure (dimensionless)
k_i	Coefficient of the term for fasting catabolism (g^{1-n_i}/yr)
K_{1i}	Instantaneous coefficient of utilization of consumed food for total production (dimensionless)
m_i	Power value of the formula relating the food consumption rate to the body weight (dimensionless)
M_i	Instantaneous rate of natural mortality (yr^{-1})
n_i	Exponent of the term for fasting catabolism in the Ursin growth equation (dimensionless)
$\overline{N}_i$	Average number of cod during 1978 (dimensionless)
N_{0i}	Number of cod at the beginning of 1978 (dimensionless)
P_i	Percent of mature cod (%)
R_j	$\frac{\partial D}{\partial u_j}$, see explanation for D and u_j (dimensionless)
ΔR_{4Ti}	Biomass of food consumed by a cod during the 8 mo of 1978 during which cod is present in NAFO area 4T (g)
ΔR_{Vn_i}	Biomass of food consumed by a cod during the 4 mo of 1978 during which cod is not present in NAFO area 4T (g)
t	Time (yr)
u_j	Relative error in the jth input parameter (dimensionless)
w_i	Current weight of a fish (g)
$\overline{w}_i$	Yearly average weight of a fish
var(D)	Variance of the D-measure, see explanation for D (dimensionless)
ΔC_i	Yearly total catabolism (g/yr)
$\Delta C_{\text{fast}.i}$	Yearly fasting catabolism (g/yr)
$\Delta C_{\text{feed}.i}$	Yearly feeding catabolism (g/yr)
ΔP_i	Yearly total production (g/yr)
ΔR_i	Yearly total food consumption (g/yr)
$\Delta R_i'$	Yearly consumption of food utilized for somatic growth and maintenance expenses (g/yr)

ΔR_{E_i} Yearly consumption of food utilized for reproduction (g/yr)

$\text{var}(u_j)$ Variance in the relative error (u_j) in the jth input parameter for the procedure (dimensionless)

Z_i Instantaneous rate of total mortality (yr^{-1})

α_i Fraction of assimilated food lost in feeding catabolism by a fish (pure number)

β_i Assimilated fraction of food consumed by a fish (dimensionless)

Appendix

Data base (not included in the proper test) required for implementing the calculations carried out in this paper.

TABLE A1. Empirical weights-at-age (in g) for 1977 (Lett 1978) and 1978 (data provided by Dr D. F. Gray), the numbers-at-age, and the instantaneous rates of fishing mortality for cod in NAFO area 4T for 1978 (Gray 1979).

Age-group[a]	Weight		Number ($\bar{N}_i$) 1978 (Jan.) (in thousands)	Instantaneous rate of fishing mortality (1978)
	1977 (Jan.)	1978 (June)		
1	—	100[b]	157 075[d]	0.00[e]
2	60	200[b]	128 602[d]	0.00[e]
3	230	380	105 291	0.01
4	480	680	130 796	0.10
5	1 030	1 040	79 142	0.19
6	1 660	1 670	28 428	0.25
7	2 410	2 260	15 483	0.25
8	3 500	2 780	5 851	0.25
9	4 280	4 050	1 157	0.25
10	4 870	4 320	1 222	0.25
11	6 240	5 850	412	0.25
12	5 680	5 540	373	0.25
13	5 970	6 260	129	0.25
14	6 000	5 040	40	0.25
15	6 000	11 711 (7 000[c])	30	0.25

[a]The ith age-group consists of fish becoming i yr old in the calendar year under consideration.

[b]Due to lack of empirical data for this particular age-group, the weight is approximately estimated with the aid of the graph displaying the relation between the body weight of cod and its age for June 1978.

[c]The value of 11 711 is not reliable as a result of the extremely small number of samples (Dr D. F. Gray, personal communication). Because this value is not consistent with growth data for the 1963 year-class of cod, the weight of 7 000 g (approximately estimated with the aid fo the graph displaying the relation between the body weight of cod and its age for the 1963 year-class) is used in the calculations performed in this paper.

[d]This number is estimated assuming that M_j for this age-group is equal to 0.2 (Gray 1979), F_i is equal to 0.0 (Dr D. F. Gray, personal communication), and the recruitment to the first age-group was the same during the period 1977–78.

[e]Dr D. F. Gray, personal communication.

An In Situ Study of Cadmium and Mercury Stress in the Plankton Community of Lake 382, Experimental Lakes Area, Northwestern Ontario[1]

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Four in situ experiments with small-volume (28-L) enclosures were conducted in Experimental Lakes Area Lake 382 to assess the effects of inorganic mercury and cadmium on the plankton community. Additions of 0.9×10^{-8} mol Cd/L caused significant reductions of crustacean zooplankton density, zooplankton community similarity, zooplankton species diversity, and dissolved oxygen concentration over 3-wk periods. Additions of 1.0×10^{-8} mol Hg/L caused reductions similar to those of 0.9×10^{-8} mol Cd/L. Phytoplankton primary productivity was reduced by additions of 2.0×10^{-8} mol Hg/L but not by 1.0×10^{-8} mol Hg/L. On a molar concentration basis, the toxicities of inorganic mercury and cadmium were quite similar. Significant changes in lake plankton communities may occur at molar concentrations above 0.2×10^{-8} mol/L. Potentially toxic concentrations of cadmium may occur in many contaminated lakes, but toxic concentrations of mercury probably occur in few lakes.

Key words: Precambrian Shield lakes, plankton communities, phytoplankton, zooplankton, cadmium, mercury toxicity

MARSHALL, J. S., J. I. PARKER, D. L. MELLINGER, AND S. G. LAWRENCE. 1981. An in situ study of cadmium and mercury stress in the plankton community of Lake 382, Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 38: 1209–1214.

Quatre expériences in situ dans des enceintes de faible volume (28 L) ont été menées dans le lac 382 de la Région des lacs expérimentaux en vue d'évaluer les effets du mercure et du cadmium inorganiques sur la communauté planctonique. L'addition de $0{,}9 \times 10^{-8}$ mol de Cd/L a causé d'importantes diminutions de densité des crustacés planctoniques, de similaritié des communautés zooplanctoniques, de diversité d'espèces zooplanctoniques et de concentration d'oxygène dissous durant des périodes de 3 semaines. L'addition de $1{,}0 \times 10^{-8}$ mol de Hg/L produisit des diminutions semblables à celles de $0{,}9 \times 10^{-8}$ mol de Cd/L. Des additions de $2{,}0 \times 10^{-8}$ mol de Hg/L résultèrent en une diminution de productivité primaire du phytoplancton, mais non l'addition de $1{,}0 \times 10^{-8}$ mol de Hg/L. Sur la base de concentration molaire, la toxicité du mercure et du cadmium inorganiques est assez semblable. Il peut se produire des changements significatis dans les communautés planctoniques des lacs à des concentrations molaires supérieures à $0{,}2 \times 10^{-8}$ mol/L. Des concentrations potentiellement toxiques de cadmium peuvent se trouver dans plusieurs lacs contaminés, alors que des concentrations toxiques de mercure se trouvent probablement dans peu de lacs.

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CADMIUM and mercury rank among the most toxic of heavy metals, and plankton may be more sensitive than other aquatic organisms to both. Cadmium is toxic to freshwater zooplankton at concentrations as low as 0.2 μg Cd/L (Marshall and Mellinger 1980a), but not to phytoplankton at less than 2 μg Cd/L (Conway 1978; Gachter 1976) or to fish at less than 1 μg Cd/L (Chapman 1978). Inorganic mercury is toxic at concentrations as low as 2 μg Hg/L to zooplankton (K. E. Biesinger, USEPA-Duluth, personal communication) and phytoplankton (Gachter 1976; Knauer and Martin 1972), but not to fish at less than 5 μg Hg/L (Brown and Parsons 1978). Methylmercury concentrations greater than 0.05 μg Hg/L are toxic to phytoplankton (Knauer and Martin 1972) and zooplankton (K. E. Biesinger personal communication) whereas methylmercury has not been reported to be toxic to fish at concentrations less than 0.9 μg Hg/L (McKim et al. 1976). In a recent marine enclosure experiment, an inorganic mercury addition of 5 μg Hg/L had pronounced effects on the zooplankton (Beers et al. 1977) whereas its long-term effects on phytoplankton (Thomas et al. 1977) and fish (Koeller and Wallace 1977) were secondary. Although several studies have been made of cadmium and mercury toxicity to various aquatic organisms, nothing has been published on their comparative chronic toxicity to a natural freshwater plankton community.

The primary purpose of this study was to assess the chronic toxicities of inorganic mercury and cadmium on the plankton community in Experimental Lakes Area (ELA) Lake 382, using the in situ experimental method developed by Marshall and Mellinger (1980b). We also investigated the sorption of added inorganic mercury and cadmium by different size fractions of the seston.

Materials and Methods

Four in situ experiments were conducted in ELA Lake 382, a small Precambrian Shield lake in the Experimental Lakes Area of northwestern Ontario. Limnological characteristics and map coordinates of Lake 382 are given in Cleugh and Hauser (1971). Field procedures were generally the same as those described by Marshall and Mellinger (1980b).

In each of two cadmium experiments, epilimnetic water (with natural plankton assemblage) was collected with a nonmetallic Kemmerer sampler from depths of 2.5−5.0 m and mixed in a 50-L container. A pair of 28-L polyethylene carboys were filled with the mixed water for each of six uncubation depths (2.5, 3.0, 3.5, 4.0, 4.5, and 5.0 m). Cadmium (as $CdCl_2$) was added to one of each pair of carboys (1 μg Cd/L) leaving the other as a depth-paired control. The cadmium spike solution contained the radioisotope ^{109}Cd as a tracer; and carrier-free ^{109}Cd ($<3.7 \times 10^{-5}$ μg Cd/L) was added to the controls. Each carboy was suspended in the epilimnion at the above designated depths for 3 wk. The two cadmium experiments were conducted consecutively during August 9−September 19, 1978. Dissolved oxygen concentration in each carboy at the end of the first experiment was measured with a YSI model 57 oxygen meter. At the end of both experiments, a 20-mL sample was removed from each carboy for determination of total ^{109}Cd and a 300-mL sample was filtered through a 0.45-μm Millipore filter for determinations of particulate and dissolved ^{109}Cd. The remaining water in each carboy was filtered through a 64-μm Nitex screen to retain a sample for quantitative zooplankton analysis as well as measurement of ^{109}Cd. Seston remaining in the filtrate (<64 μm) was separated into three additional size fractions by filtering 300-mL subsamples through 10-μm or 28-μm Nitex screens or a 0.45-μm Millipore filter. Stable cadmium concentrations (ng Cd/L) were calculated from the results of the ^{109}Cd measurements by assuming isotopic equilibrium in the controls as well as the Cd-treated carboys. Total cadmium concentration in the controls (ambient lake concentration) was assumed to be 50 ng Cd/L, based on the finding of <100 ng Cd/L in ELA Lake 382 by Beamish et al. (1976).

In each of two mercury experiments, four carboys for each of three incubation depths (3.0, 3.5, and 4.0 m) were filled as in the cadmium experiments. Mercury (as $HgCl_2$) was added to three of the carboys for each depth (1, 2, and 4 μg Hg/L), leaving one carboy as a control for each depth. The mercury (containing ^{203}Hg as a radiotracer in the first experiment only) was added with a serological pipet. Controls in the first experiment were spiked with $<3.7 \times 10^3$ Bq ^{203}Hg of high specific activity (5.6×10^4 Bq/μg), thus increasing the stable mercury concentration by less than 0.07 μg Hg/L. The mercury concentration in the controls prior to the ^{203}Hg addition was assumed to be <0.02 μg Hg/L, the value reported to be typical for unpolluted lakes (Armstrong 1980). The carboys were suspended in the epilimnion at the designated depths for 3 wk. The two mercury experiments were conducted consecutively during July 3−August 14, 1979. Dissolved oxygen concentrations were measured at the end of both experiments with a YSI model 57 oxygen meter. At the end of the second experiment, 2-L samples from control and Hg-treated carboys (2 and 4 μg Hg/L) from depths of 3.0 and 4.0 m were taken for primary productivity measurements at the ELA laboratory. Samples for determinations of particulate, dissolved, and total ^{203}Hg concentrations at the end of the first experiment were prepared as described above for the ^{109}Cd samples. Stable mercury concentrations (μg Hg/L) were calculated from the results of the ^{203}Hg measurements by assuming isotopic equilibrium in the controls as well as Hg-treated carboys.

In the laboratory, ^{203}Hg concentrations were determined by gamma-ray spectrometry using a NaI detector. Primary productivity was determined by the ^{14}C method using an incubator described by Fee (1973). Zooplankton were identified from keys and descriptions in Edmondson (1959). Quantitative zooplankton analyses were made by counting one-fourth or more of each sample in a chambered counting cell (Gannon 1971). Two similarity indices (the coefficient of community, *CC*, and percentage similarity, *PS*) and three species diversity indices (Hill's numbers N_0, N_1, and N_2) were calculated for the crustacean zooplankton community as described in Marshall and Mellinger (1980a).

Results

Inorganic mercury and cadmium had significant effects on zooplankton populations, zooplankton community structure, phytoplankton primary productivty, and dissolved oxygen

TABLE. 1. Average densities of different categories of crustacean zooplankton (mean numbers per litre ± standard errors) for control and metal-treated enclosures in 3-wk in situ experiments with cadmium (August 9–September 19, 1978) and mercury (July 3–August 14, 1979) in ELA Lake 382. Numbers in parentheses indicate number of enclosures. Underlined values are significantly different from controls ($P < 0.05$).

Category	Cadmium additions		Mercury additions			
	0 μg Cd/L (12)	1 μg Cd/L (12)	0 μg Hg/L (6)	1 μg Hg/L (6)	2 μg Hg/L (6)	4 μg Hg/L (6)
Cladocera						
Diaphanosoma spp.	0.9±0.2	0.2±0.1	0.5±0.2	0.5±0.2	0.1±0.1	0.02±0.02
Holopedium gibberum	1.1±0.2	0.02±0.02	0	0	0	0
Sida crystallina	0	0	0.3±0.03	0.05±0.05	0.2±0.2	0
Bosmina longirostris	4.6±0.8	4.1±1.0	19.0±4.6	24.4±7.0	21.7±4.4	5.2±2.8
Daphnia galeata mendotae	2.4±0.6	2.3±0.5	3.4±0.5	3.1±0.6	1.5±0.5	0.5±0.2
Chydorus sphaericus	4.1±0.6	3.4±0.9	19.4±7.6	15.3±6.3	13.9±6.8	18.5±7.1
Copepoda						
Cyclops vernalis	0.7±0.1	0.7±0.2	0.9±0.3	0.7±0.2	1.0±0.2	0.9±0.3
Mesocyclops edax	0.3±0.1	0.2±0.1	0.4±0.1	0.5±0.2	0.6±0.1	0.5±0.1
Tropocyclops prasinus mexicanus	0.4±0.1	0.5±0.1	0.3±0.1	0.3±0.1	0.2±0.1	0.02±0.05
Cyclopoid copepodites I–V	2.7±0.3	2.1±0.4	1.6±0.4	1.1±0.3	1.1±0.4	0.8±0.2
Diaptomus minutus	0.4±0.1	0.3±0.1	3.4±1.0	3.7±1.3	3.5±1.3	4.2±1.2
Epischura lacustris	0.1±0.01	0.04±0.03	0	0.03±0.03	0.08±0.05	0.07±0.04
Calanoid copepodites I–V	6.5±0.6	5.7±0.5	6.3±0.8	7.0±1.0	7.8±1.2	6.7±1.4
Total Crustacea	24.3±2.1	19.8±1.9	54.7±10.3	56.9±10.6	51.4±6.9	37.5±7.4

TABLE. 2. Average values of two indices of community similarity (*CC* and *PS*) and three indices of species diversity (N_0, N_1, and N_2) for crustacean zooplankton in control and metal-treated enclosures (means ± SE) in 3-wk in situ experiments with cadmium (August 9–September 19, 1978) and mercury (July 3–August 14, 1979) in ELA Lake 382. Numbers in parentheses indicate number of enclosures. Underlined values are significantly different from controls ($P < 0.5$).

Index	Cadmium additions		Mercury additions			
	0 μg Cd/L (12)	1 μg Cd/L (12)	0 μg Hg/L (6)	1 μg Hg/L (6)	2 μg Hg/L (6)	4 μg Hg/L (6)
CC	93.5±1.6	86.8±1.4	95.8±0.8	94.3±0.8	90.0±2.8	85.0±3.9
PS	83.8±1.2	78.3±2.2	90.5±1.5	84.9±2.6	82.4±4.0	66.6±6.8
N_0	11.0±0.4	9.6±0.3	9.7±0.2	10.0±0.4	9.5±0.3	8.3±0.4
N_1	6.6±0.4	5.7±0.4	5.0±0.6	4.6±0.5	4.1±0.4	3.4±0.2
N_2	5.1±0.4	4.4±0.4	3.7±0.5	3.6±0.4	3.1±0.3	2.5±0.2
N_2:N_1[a]	0.77±0.02	0.76±0.04	0.75±0.04	0.78±0.01	0.75±0.02	0.75±0.03

[a]An index of evenness (Hill 1973)

concentration. Average densities of different categories of crustacean zooplankton and average values of the indices of community similarity (*CC* and *PS*) and species diversity (N_0, N_1, and N_2) were affected similarly in the two experiments with each metal, so only the overall mean values for each pair of experiments combined are presented (Tables 1 and 2). The normalized *PS* value for carboys treated with 0.9×10^{-8} mol Cd/L (1 μg Cd/L) falls close to the regression line calculated from the mercury data and is not significantly different from the value for carboys treated with 1.0×10^{-8} mol Hg/L (2 μg Hg/L) (Fig. 1). The normalized value of N_1 for carboys treated with 0.9×10^{-8} mol Cd/L likewise falls very close to the regression line calculated from the mercury data and is not significantly different from the value for carboys treated with 1.0×10^{-8} mol Hg/L (Fig. 2). Reductions of N_1 were mainly due to reduced species richness. The evenness component of diversity, as indicated by the N_2:N_1 ratio (Hill 1973), was not significantly affected (Table 2). Dissolved oxygen concentration was significantly reduced, relative to controls, in carboys treated with cadmium (*t*-test, $P < 0.05$) but was not significantly reduced by any of the mercury treatments. Dissolved oxygen in controls was 98 ± 2% saturation. Primary productivity was reduced by 36% in carboys treated with 4 μg Hg/L (*t*-test, $P < 0.05$) but was not significantly reduced in those treated with 2 μg Hg/L.

Cadmium concentrations sorbed by the total seston (>0.45 μm) were less than 10% of the added cadmium (Table 3) whereas the concentration of mercury sorbed by the total seston was about 60% of the added mercury (Table 4). From 75 to 100% of the added mercury appeared to remain in the unfiltered water (not sorbed onto carboy walls) after 3 wk (Table 4). The coarse seston containing the crustacean zooplankton (>64 μm) sorbed only ~3% of the added cadmium (Table 3) and ~4% of the added mercury (Table 4).

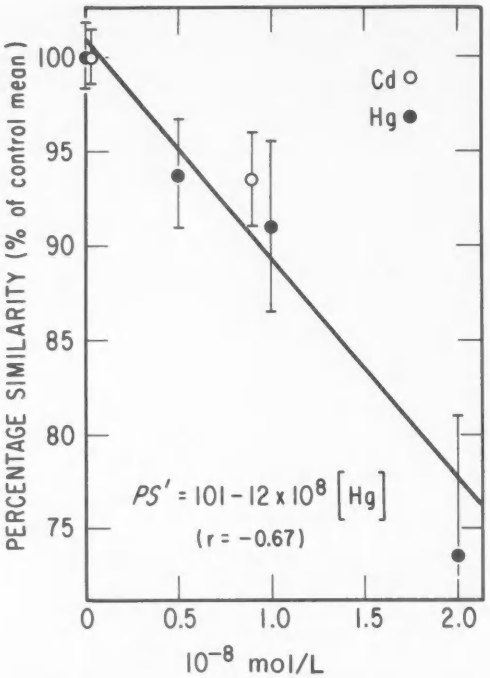

FIG. 1. A comparison of the effects of added inorganic mercury and cadmium, both in molar concentrations, on the percentage similarity index (% of mean values for controls) for crustacean zooplankton after 3-wk in situ incubations in small enclosures in ELA Lake 382.

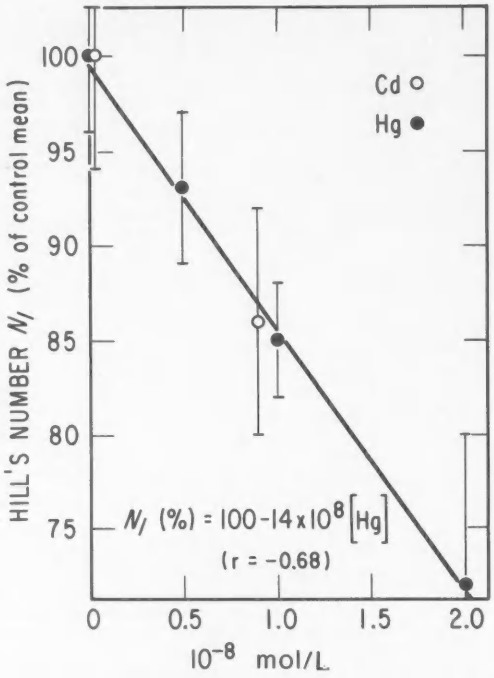

FIG. 2. A comparison of the effects of added inorganic mercury and cadmium, both in molar concentrations, on Hill's number N_1 (% of mean values for controls) for crustacean zooplankton after 3-wk in situ incubations in small enclosures in ELA lake 382.

Discussion

The effects of cadmium additions of 1 μg Cd/L on crustacean zooplankton density, zooplankton community similarity, species diversity, and dissolved oxygen concentration are similar to those reported by Marshall and Mellinger (1980a) for additions of 0.8−1.2 μg Cd/L in Lake Michigan and ELA Lake 223 experiments after 3 wk. The percentage reduction of total crustacean density (~18%) was close to that predicted from Lake Michigan data. *Holopedium gibberum*, the species reduced most in the ELA Lake 382 experiments, was also one of the most severely reduced species in the Lake Michigan experiments. The mean value of *PS* for the ELA Lake 382 experiments fell within the 95% confidence limits for values predicted from Lake Michigan data and was not significantly different from the 3-wk *PS* value for zooplankton in a large limno-corral in ELA Lake 223 treated with 1 μg Cd/L (Marshall and Mellinger 1980a). The average percentage reduction of dissolved oxygen concentration (~3%) was also close to that predicted from Lake Michigan data.

The effects of inorganic mercury additons (1−4 μg Hg/L) on the plankton in ELA Lake 382 were consistent with the results of previous studies. However, chronic mercury toxicity has sometimes been underestimated due to mercury sorption onto container walls or volatilization. For example,

TABLE. 3. Concentrations of sorbed cadmium (ng Cd/L) in different size fractions of the seston in control and Cd-treated (1 μg Cd/L) enclosures after 3-wk incubations in ELA Lake 382, August 9−30, 1978 (experiment I) and August 30−September 19, 1978 (experiment II).

Seston size fraction, μm	Experiment I		Experiment II	
	Controls	Treated	Controls	Treated
>64	2±1	24±5	3±1	25±5
28−64	1±1	20±3	1±1	20±7
10−64	3±1	22±7	3±1	41±5
0.45−64	14±1	95±14	3±1	45±6
>0.45	10±2	98±14	3±1	50±9

Biesinger and Christensen (1972) reported significant reproductive impairment of *Daphnia magna* in chronic (3-wk) tests at added, but unmeasured, mercury concentrations as low as 3.4 μg Hg/L. In later tests, significant reproductive impairment of *D. magna* was found at measured mercury concentrations as low as 1.8 μg Hg/L (K. E. Biesinger personal communication). As we found significant reductions of *Daphnia galeata mendotae* populations from additions as low as 2 μg Hg/L (of which ~1.5 μg Hg/L remained in the water after 3 wk), our results are consistent with those for

TABLE. 4. Total mercury concentrations remaining in unfiltered water and concentrations of mercury sorbed by total seston (>0.45 μm) and coarse seston (>64 μm) in control and Hg-treated enclosures after a 3-wk incubation in ELA Lake 382, July 3–24, 1979. Values in parentheses indicate percentage of added mercury represented by mercury concentrations shown.

Added Hg (μg/L)	Total Hg after 3 wk (μg/L)	Total seston Hg >0.45 μm (μg/L)	Coarse seston Hg >64 μm (μg/L)
0	<0.05	<0.03	<0.02
1	1.0 (100)	0.6±0.04 (60)	0.04±0.003 (4)
2	1.5 (75)	1.1±0.03 (55)	0.06±0.015 (3)
4	3.2 (80)	2.6±0.02 (65)	0.16±0.035 (4)

D. magna. Our evidence for reduced primary productivity from additions of 4 μg Hg/L is also consistent with previous findings, but the toxicity of mercury to freshwater phytoplankton appears to vary greatly. Gachter (1976) found that the mercury concentration required to reduce primary productivity by 20% in 24 h in two Swiss lakes varied seasonally from 1 to 14 μg Hg/L, and the average concentrations required for the lakes differed twofold. Blinn et al. (1977) found seasonal differences in the effects of mercury on primary productivity in 24-h experiments in an Arizona lake, but >50 μg Hg/L was always required.

The relative toxicities of inorganic mercury and cadmium to planktonic organisms also is variable. In the present study, the effects of additions of 1.0×10^{-8} mol Hg/L on the zooplankton were quite similar to those of 0.9×10^{-8} mol Cd/L. However, mercury was less toxic than cadmium to *Daphnia magna* in chronic (3-wk) tests (Biesinger and Christensen 1972). Mercury was also less toxic than cadmium in chronic tests with *Chlorella vulgaris* (Hutchinson 1973; Rosko and Rachlin 1977), although mercury toxicity was probably underestimated due to sorption onto container walls. In contrast, mercury was more toxic than cadmium in acute (24-h) tests with phytoplankton from two Swiss lakes during most months (Gachter 1976). Seasonal variation in toxicity was thought to be mainly due to succession of the phytoplankton species composition (Gachter 1976). One mechanism underlying seasonal variation in toxicity is suggested by the correlations between specific algae and heavy metal binding reported by Briand et al. (1978).

Cadmium and mercury may have similar toxicities to lake plankton on a molar concentration basis, but only cadmium has been reported to occur in concentrations potentially toxic to plankton in lakes. Because of the close agreement of results of experiments in ELA lakes and Lake Michigan, cadmium concentrations ≥0.2 μg Cd/L probably are potentially toxic to plankton in many lakes. In Canada, concentrations ≥0.2 μg Cd/L have been reported in lakes near Sudbury, Ontario (Beamish and Van Loon 1977) and Flin Flon, Manitoba (Van Loon and Beamish 1977; McFarlane and Franzin 1978; Franzin and McFarlane 1980). However, cadmium toxicity may be ameliorated by zinc because zinc suppresses cadmium uptake by plankton at normal Zn:Cd ratios (Marshall et al. 1981). In contrast with cadmium, potentially toxic concentrations of inorganic mercury (≥0.4 μg Hg/L) or methylmercury (≥0.04 μg Hg/L) may not occur in lakes. In Clay Lake (one of Canada's most heavily contaminated lakes) the highest total mercury found in the water in 1972 was 0.17 μg Hg/L (Armstrong and Hamilton 1973). The highest total mercury found recently in Clay Lake was only 0.04 μg Hg/L, of which less than 5% was methylmercury (J. W. M. Rudd, Freshwater Institute, Winnipeg, personal communication).

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ARMSTRONG, F. A. J. 1980. Mercury in the aquatic environment, p. 84–100. *In* Effects of mercury in the Canadian environment. Publication NRCC 16739. National Research Council of Canada, Environmental Secretariat, Ottawa.

ARMSTRONG, F. A. J., AND A. L. HAMILTON. 1973. Pathways of mercury in a polluted northwestern Ontario lake, chapter 5, p. 131–156. *In* P. C. Singer [ed.] Trace metals and metal organic interactions in natural waters. Ann Arbor Science Publications, Ann Arbor, MI.

BEAMISH, R. J., L. M. BLOUW, AND G. A. MCFARLANE. 1976. A fish and chemical study of 109 lakes in the Experimental Lakes Area (ELA), northwestern Ontario, with appended reports on lake whitefish ageing errors and the northwestern Ontario baitfish industry. Fish. Mar. Serv. Res. Dev. Tech. Rep. 607. 116 p.

BEAMISH, R. J., AND R. C. VAN LOON. 1977. Precipitation loading of acid and heavy metals to a small lake near Sudbury, Ontario. J. Fish. Res. Board Can. 34: 649–658.

BEERS, J. R., M. R. REEVE, AND D. G. GRICE. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. IV. Zooplankton population dynamics and production. Mar. Sci. Comm. 3: 355–394.

BIESINGER, K. E., AND G. M. CHRISTENSEN. 1972. Effects of various metals on survival, growth, reproduction, and metabolism of *Daphnia magna*. J. Fish. Res. Board Can. 29: 1691–1700.

BLINN, D. W., T. TOMPKINS, AND L. ZALESKI. 1977. Mercury inhibition on primary productivity using large volume plastic cylinders *in situ*. J. Phycol. 13: 58–61.

BRIAND, F., R. TRUCCO, AND S. RAMAMOORTHY. 1978. Correlations between specific algae and heavy metal binding in lakes. J. Fish. Res. Board Can. 35: 1482–1485.

BROWN, D. A., AND T. R. PARSONS. 1978. Relationship between cytoplasmic distribution of mercury and toxic effects to zooplankton and chum salmon (*Oncorhynchus keta*) exposed to mercury in a controlled ecosystem. J. Fish. Res. Board Can. 35: 880–884.

CHAPMAN, G. A. 1978. Toxicities of cadmium, copper, and zinc to four juvenile stages of chinook salmon and steelhead. Trans. Am. Fish. Soc. 107: 841–847.

CLEUGH, T. R., AND B. W. HAUSER. 1971. Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 129–137.

CONWAY, H. L. 1978. Sorption of arsenic and cadmium and their effects on growth, micronutrient utilization, and photosynthetic pigment composition of *Asterionella formosa*. J. Fish. Res. Board Can. 35: 286–294.

EDMONDSON, W. T. [ed.] 1959. Freshwater biology, 2nd ed. John Wiley and Sons, Inc., New York, NY.

FEE, E. J. 1973. A numerical model for determining integral primary

productivity and its application to Lake Michigan. J. Fish. Res. Board Can. 30: 1447–1468.

FRANZIN, W. G., AND G. A. MCFARLANE. 1980. Elevated Zn, Cd, and Pb concentrations in waters of ice-covered lakes near a base metal smelter during the snow melt, April 1977. Environ. Pollut. Ser. B 2: 11–19.

GACHTER, R. 1976. Untersuchungen uber die Beeinflussung der planktischen Photosynthese durch anorganische Metallsalze im eutrophen Alpnachersee und der mesotrophen Horwer Bucht. Schweiz. Z. Hydrol. 38: 97–119.

GANNON, J. E. 1971. Two counting cells for the enumeration of zooplankton microcrustacea. Trans. Am. Microsc. Soc. 90: 486–490.

HILL, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432.

HUTCHINSON, T. C. 1973. Comparative studies of the toxicities of heavy metals to phytoplankton and their synergistic interactions. Water Pollut. Res. Can. 8: 68–90.

KNAUER, G. A., AND J. H. MARTIN. 1972. Mercury in a pelagic marine food chain. Limnol. Oceanogr. 17: 868–876.

KOELLER, P. A., AND G. T. WALLACE. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. V. Growth of juvenile chum salmon (*Oncorhynchus keta*). Mar. Sci. Comm. 3: 395–406.

MARSHALL, J. S., AND D. L. MELLINGER. 1980a. Dynamics of cadmium-stressed plankton communities. Can. J. Fish. Aquat. Sci. 37: 430–414.

1980b. An *in situ* experimental method for toxicological studies on natural plankton communities, p. 27–39. *In* J. G. Eaton, P. R. Parrish, and A. C. Hendricks [ed] Aquatic toxicology, ASTM STP 707. American Society for Testing and Materials, Philadelphia, PA.

MARSHALL, J. S., D. L. MELLINGER, AND J. I. PARKER 1981. Combined effects of cadmium and zinc on a Lake Michigan zooplankton community J. Great Lakes Res. (In press)

MCFARLANE, G. A. AND W. G. FRANZIN. 1978. Elevated heavy metals: a stress on a population of white sucker, *Catostomus commersoni*, in Hamell Lake, Saskatchewan. J. Fish. Res. Board Can. 35: 963–970.

MCKIM, J. M., G. F. OLSON, G. W. HOLCOMBE, AND E. P. HUNT. 1976. Long-term effects of methylmercuric chloride on three generations of brook trout (*Salvelinus fontinalis*): toxicity, accumulation, distribution, and elimination. J. Fish. Res. Board Can. 33: 2726–2739.

ROSKO, J. J., AND J. W. RACHLIN. 1977. The effect of cadmium, copper, mercury, zinc, and lead on cell division, growth, and chlorophyll *a* content of the chlorophyte *Chlorella vulgaris*. Bull. Torrey Bot. Club 104: 226–233.

THOMAS, W. H., D. L. R. SEIBERT, AND M. TAKAHASHI. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. III. Phytoplankton population dynamics and production. Mar. Sci. Comm. 3: 331–354.

VAN LOON, J. C., AND R. C. BEAMISH. 1977. Heavy-metal contamination by atmospheric fallout of several Flin Flon area lakes and the relation to fish populations. J. Fish. Res. Board Can. 34: 899–906.

Orthophosphate and its Flux in Lake Waters

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Molybdate reactive high molecular weight (MW > 5000) phosphorus (RHMW-P) in solution was separated from low molecular weight material (PO_4-P) by Sephadex gel (G25–150). PO_4-P is as close to orthophosphate as has been possible to achieve with molybdenum blue technology. Chromatograms of near-surface waters of 32 lakes showed that RHMW-P was rarely the dominant component of dissolved reactive phosphorus (DRP), and so cannot be the major influence causing discrepant estimates of orthophosphate concentrations derived from molybdenum blue and radiotracer technology. The low molecular weight material (PO_4-P) may still contain chemically reactive organic phosphorus which could lead to overestimation of orthophosphate. Recent literature points to discrepancies in radiotracer estimates too, so further effort is required to provide reliable assessment of orthophosphate in lake water. Estimates of orthophosphate flux from solution to particulate material based on $^{32}PO_4$-derived turnover times are likely to be in error irrespective of the source of orthophosphate estimate.

Key words: molybdenum blue method, radiotracer, orthophosphate flux, reactive high molecular weight phosphorus, gel chromatography, radiobioassay

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Nous avons utilisé le gel Sephadex (G25–150) pour séparer le phosphore de poids moléculaire élevé (PM > 5000) réagissant au molybdate en solution du matériel de faible poids moléculaire (P-PO_4). Le P-PO_4 se rapproche le plus de l'orthophosphate en autant qu'une technologie au bleu de molybdène le permette. Des chromatogrammes d'eaux de près de la surface de 32 lacs démontrent que le phosphore de poids moléculaire élevé (RHMW-P) est rarement l'élément dominant du phosphore réactif dissous (DRP). Il ne peut donc pas être la cause principale des différences dans l'estimation des concentrations d'orthophosphate par bleu de molybdène et par marquage radioactif. Le matériel de faible poids moléculaire (P-PO_4) peut toujours contenir du phosphore organique chimiquement réactif capable de causer une surestimation de l'orthophosphate. Les récents travaux publiés font ressortir les différences dans les estimations par marquage radioactif également, de sorte qu'il faudra poursuivre les études qui conduiront à une évaluation fiable de l'orthophosphate dans l'eau des lacs. Quelle que soit la source de l'estimation de l'orthophosphate, il y aura probablement erreur dans l'estimation du flux d'orthophosphate de la solution au matériel particulaire fondée sur les temps de renouvellement dérivés de $^{32}PO_4$.

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THE validity of the molybdenum blue technique for measuring dissolved orthophosphate in aquatic ecosystems has been questioned since Kuenzler and Ketchum (1962) and Rigler (1966, 1968) suggested that this method exaggerated the concentration of dissolved orthophosphate by 10–100 times. Rigler suggested that interfering elements and/or organic phosphorus material hydrolyzed by the acid reagents were responsible for the overestimation. Improved analytical techniques have been developed (Johnson 1971; van Schouwenburg and Walinga 1967; Downes 1978) to avoid interference by elements such as arsenic, silicon, mercury, and germanium.

Downes and Paerl (1978) used technology which excluded metal interference, but found dissolved chemically reactive phosphorus (DRP) emerging with the void volume when fil-

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tered lake water was chromatogrammed with Sephadex G-25 coarse gel. They stated that this reactive high molecular weight phosphorus (RHMW-P) was likely to be responsible for the overestimation of orthophosphate in natural waters. They equated the low molecular weight phosphorus in the chromatogram with orthophosphate. Many of the characteristics of the RHMW-P corresponded to those hypothesized by Rigler (1968).

Bioassays (Paerl and Downes 1978) showed that their low molecular weight phosphorus was utilized by phosphorus-starved *Chlorella* in preference to RHMW-P, but given time all of the DRP was used. In a more extensive series of bioassays using similar technology, White and Payne (1980) confirmed the preferred uptake of the low molecular weight material and demonstrated that although the growth responses of algae to orthophosphate, low molecular weight material, and RHMW-P uptake were equivalent quantitatively, some RHMW-P remained in solution after the algae ceased to grow, indicating that not all of it was available for growth.

White and Payne (1980) succeeded in quantitatively fractionating some lake surface waters with low DRP concentrations (<2 mg·m^{-3}) into RHMW-P and low molecular weight material. They pointed out that if Downes and Paerl (1978) were right in stating that RHMW-P caused the orthophosphate overestimation postulated by Rigler (1966, 1968), the relative abundance of RHMW-P to orthophosphate would often favor the RHMW-P by 10- to 100-fold, particularly where $^{32}PO_4$-derived turnover times (TT) for the phosphate pool were rapid. Their early findings did not support this; the low molecular weight fraction was usually larger than the RHMW-P fraction. They conceded that short turnover times were rare in the lakes they studied and suggested that examination of "Rigler's lakes" using Sephadex chromatography in combination with continuous-flow DRP analysis might resolve the issue.

The present paper examines the relative distribution of RHMW-P and low molecular weight phosphorus (PO_4-P) in lake waters, together with turnover times and supposed flux of phosphate between solution and particulate material. Most of the work was done with waters from lakes of the central volcanic plateau of the North Island of New Zealand, but there were also single examinations of seven lakes from Westland in the South Island of New Zealand, and occasional studies of lakes in Ontario, Canada, including those studied by Rigler (1964).

Materials and Methods

The lake water samples were taken within 0.5 m of the surface. Most were 5-L samples, collected in acid-washed polythene bottles and processed in the laboratory within 2 h of collection. All laboratory glassware was soaked in acid, washed in distilled–deionized water, and oven-dried before use.

Filters, 0.45-μm porosity Millipore or Sartorius, were soaked in 1 mol·L^{-1} HCl and washed in the filter holders with distilled–deionized water immediately before use. Analyses of particulate phosphorus (PP) were carried out on GF/C filters. Partial vacuums of 16–27 kPa were used in filtrations.

Sephadex chromatography of samples utilized G25–150 (fractionating range, MW 100–5000), a medium gel in a column 26 cm long and 2 cm in diameter, at measured flow rates approximating 2 mL·min^{-1} (White and Payne 1980). Waters to be chromatographed were filtered immediately before being applied to the column. The eluant was 0.2% sodium chloride with 0.03% sodium azide.

Carrier-free $^{32}PO_4$ in the form of phosphoric acid was used for all the radioisotope studies. Measurements of radioactivity were made with a Beckman LS100C liquid scintillation counter; Cerenkov counting was employed.

DRP content of filtered lake water and of molybdate reactive phosphorus eluted from Sephadex columns was estimated from the color developed using Technicon AutoAnalyzer II equipment and the method of Downes (1978).

For PP analyses, the GF/C filter with particulate material was placed in a Pyrex digestion tube (9 cm long and 1.5 cm in diameter) and frozen for subsequent batch analysis. Each batch was digested in a heated aluminum block for 3 h. The digestion mixture was 0.5 mL of a solution of selenium, hydrated copper sulfate, and potassium sulfate in concentrated H_2SO_4 (1.04 g Se, 2.4 g $CuSO_4 \cdot 5H_2O$, 68 g K_2SO_4, 100 mL conc. H_2SO_4). After digestion, the fluid was diluted to 10 mL with distilled–deionized water and was mixed vigorously. The phosphate was analyzed using the automated method of Downes (1978), with adjustments made to the volume of sample and to the acidity and volume of reagents to obtain the specified final acidity.

Downes (1978) estimated the standard deviation of eight analyses of DRP in lake water which had an average absorbance equivalent to 0.31 mg P·m^{-3} as 0.18 mg P·m^{-3}. We found the standard deviation of 36 replicate analyses of water from Lake Rerewhakaaitu with a mean DRP concentration of 0.26 mg·m^{-3} was 0.024 mg·m^{-3}; the range of estimated concentration was 0.19–0.30 mg·m^{-3}. PP analyses are more variable, so were always done in duplicate and occasionally in quadruplicate. Recent experience with the Sephadex column and attached phosphorus analytical system shows that when the whole system is working well, concentrations as low as 0.15 mg P·m^{-3} can be identified.

The experiments to determine turnover times of the orthophosphate pool in solution were usually terminated at 120 min. Samples with the seston killed by formaldehyde (final concentration 0.15%) were used as controls against which biotic uptake was measured. Initial uptake rate constants used to estimate flux of PO_4-P from solution to seston were calculated from data collected in the first 2 min if the turnover time was short. Where this time was long, data collected over a longer time were used in calculation of the uptake rate constant. Uptake was presumed to proceed exponentially. A summary of all data can be obtained from the authors upon request.

Results and Discussion

A total of 67 chromatograms was obtained from near-surface water samples of 32 lakes. Twenty-six of the samples contained enough RHMW-P and PO_4-P to allow precise estimation of the relative abundance of the phosphorus forms. In seven of these samples, from Lakes Ngahewa,

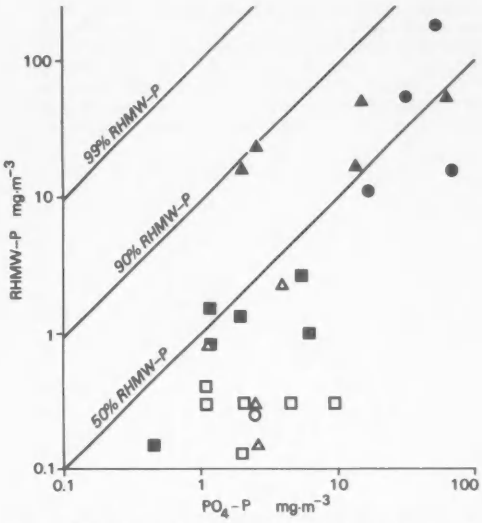

FIG. 1. The relative distribution of RHMW-P and PO_4-P in lake surface water samples. ▲, L. Ngahewa; ●, L. Tutaeinanga; ○, L. Rerewhakaaitu; □, L. Rotorua; △, L. Okaro; ■, others.

Tutaeinanga, and Teapot, RHMW-P made up more than 50% of the DRP (Fig. 1). The other 19 samples contained more PO_4-P than RHMW-P. Of the 41 samples which contained concentrations of DRP which were too small to allow precise assessment of RHMW-P and PO_4-P, the latter form was always more abundant.

Hydrolysis of high molecular weight phosphorus material by acid in color reagents certainly leads to overestimation of orthophosphate (Downes and Paerl 1978; Stainton 1980), but in our samples this was not usually of the order postulated by Rigler (1966, 1968). If our estimates of PO_4-P approximate orthophosphate, then the ratio of RHMW-P/PO_4-P required to accommodate Rigler's hypothesis would be of the order of 10–100. This was approached only in the two samples from Lake Ngahewa where about 90% of the DRP was RHMW-P (Fig. 1). It was more usual for the ratio to be less than one, particularly in samples where DRP concentrations were low and turnover times were fast.

Lake Rerewhakaaitu water always exhibits rapid uptake of $^{32}PO_4$ from solution to particulate material. On three separate occasions Rigler radiobioassays of this lake's water suggested ambient levels of orthophosphate equal to, or less than, 0.10, 0.05, and 0.20 $mg \cdot m^{-3}$, while chromatograms revealed PO_4-P concentrations of 0.98, 1.10, and 1.05 $mg \cdot m^{-3}$, respectively. For this lake water our best estimates of orthophosphate (PO_4-P) are at least 5 to 20 times greater than radiobioassay estimates.

Indirect evidence suggest that these discrepancies in estimates are likely to be general rather than specific to Lake Rerewhakaaitu. Our data from Ontario lakes (Table 1) show turnover times and DRP concentrations that were generally comparable to those found by Rigler (1964) in the early 1960s. The exception was Grenadier Pond, where both of our samples showed little uptake of $^{32}PO_4$ and one contained an abundance of DRP in solution (9.13 $mg \cdot m^{-3}$). Chromatograms revealed that RHMW-P was present in some of the Ontario lakes. Traces (0.15–0.30 $mg \cdot m^{-3}$) were found in samples from Mary, Heart, and Thompson lakes. The samples from Teapot Lake contained 2.67 and 1.51 $mg \cdot m^{-3}$ RHMW-P, which amounted to 32 and 56% of the DRP, respectively, and Two Rivers Lake contained 0.75 $mg \cdot m^{-3}$ RHMW-P, 37% of the DRP. RHMW-P was not detected (<0.15 $mg \cdot m^{-3}$) in the remaining five lakes. Rigler (1966) provided three chemical and radiobioassay estimates of dissolved inorganic phosphorus in Grenadier Pond, Heart Lake, and Thompson Lake. His chemical estimates generally compare with ours for DRP but his maximal estimates of orthophosphate derived from radiobioassays were almost always much smaller than our PO_4-P estimates.

Flux rates, calculated by combining the reciprocal of $^{32}PO_4$-derived turnover times with our PO_4-P estimates, show a wide range of variability but, where multiple assessments are available, the differences between lakes appear greater than the variability within lakes (Table 2) and the turnover times seem to influence assessments of flux more than PO_4-P or PP concentrations. When turnover times are short, flux is usually high (>10 $mg \cdot m^{-3} \cdot h^{-1}$), substantially higher than flux found in studies using radiobioassay-derived estimates of orthophosphate. Levine and Schindler (1980) estimated flux this way for 2 yr in epilimnetic waters of Lakes 227 and 302S, and rarely found rates in excess of 0.3 and never more than 1.0 $mg \cdot m^{-3} \cdot h^{-1}$. By contrast, our flux estimates for Ontario lakes (Table 1) were enormous whenever turnover times were short. These differences are unlikely to be related solely to differences between the lakes; the major difference almost certainly lies with the different estimates of orthophosphate derived by radiobioassay and our PO_4-P.

It is concluded that in most situations removal of RHMW-P from estimates of DRP is insufficient to eliminate the discrepancy between radiobioassay and our molybdenum blue (PO_4-P) estimates of orthophosphate.

Our flux rates from solution to seston usually appear large relative to PP, and will be even larger relative to the phosphorus in the biotic component of the seston, so that turnover times for phosphorus in biota are often incredibly short. The possibility exists that PO_4-P includes dissolved organic phosphorus material of small molecular weight which elutes from the chromatographic column like orthophosphate. Certainly the short chromatographic column used in this study does not separate the $X^{32}P$ of Lean (1973) from $^{32}PO_4$, so that if XP material is molybdate reactive it will be included in our PO_4-P. However, it is also possible that the large flux rates estimated by us are in error not because PO_4-P overestimates orthophosphate, but because initial phosphate uptake rate constants (1/TT) provide inappropriate descriptions of uptake by the lake water community as a whole. Lean (1981) showed that when $^{32}PO_4$-derived turnover times are short, they are often dictated largely by small particulate material (retained by 0.2-μm Nuclepore filters but passing 1-μm Nuclepore filters), presumably bacteria. In such circumstances estimates of flux from solution to seston are likely to be dubious irrespective of the source of orthophosphate estimate. Lean also demonstrated that when particulate material in lake water is

TABLE. 1. $^{32}PO_4$-derived turnover times, chemical measurements of phosphorus, and estimates of flux between solution and seston in some Ontario lakes during August, 1979.

Lake	$^{32}PO_4$ TT (min)	DRP ($mg \cdot m^{-3}$)	RHMW-P ($mg \cdot m^{-3}$)	PO_4-P ($mg \cdot m^{-3}$)	PP ($mg \cdot m^{-3}$)	Flux ($mg \cdot m^{-3} \cdot h^{-1}$)
Mary	2.7	0.82	<0.15	0.67–0.82	10.5	14.89–18.20
	1.1	0.42	0.15–0.30	0.12–0.27	23.5	6.55–14.73
Teapot	—	8.30	2.67	5.63	222	—
	1.1	2.70	1.51	1.20	159	65.45
Heart	4.2	0.64	0.15–0.30	0.34–0.49	16.2	4.86–7.00
	2.4	0.33	<0.15	0.18–0.33	43.5	4.50–8.25
Grenadier Pond	⩾60	9.13	<0.15	8.98–9.13	33.4	0.0
	27	0.85	<0.15	0.70–0.85	36.3	1.56–1.89
St. George	1.5	1.00	<0.15	0.85–1.00	14.3	34.00–40.00
	1.3	0.37	<0.15	0.22–0.37	4.4	10.15–17.08
Thompson	0.9	0.45	<0.15	0.30–0.45	28.1	20.00–30.00
	1.2	0.61	0.15–0.30	0.31–0.46	27.6	15.50–23.00
Opeongo	—	0.35	<0.1	0.20–0.35	4.3	—
Eos	3.4	0.10	<0.15	⩽0.10	5.6	⩽1.76
Found	15.9	0.35	<0.15	0.20–0.35	2.0	0.75–1.32
Costello	—	0.25	<0.15	0.10–0.25	4.4	—
Two Rivers	>60	2.02	0.75	1.27	3.2	0.17

TABLE. 2. The range of variability in phosphorus data for a selection of lakes.

Lake	No. of observations	Turnover time (min)	RHMW-P ($mg \cdot m^{-3}$)	PO_4-P ($mg \cdot m^{-3}$)	PP ($mg \cdot m^{-3}$)	Flux ($mg \cdot m^{-3} \cdot h^{-1}$)
Rotorua	7	34.5–⩾120	0.00–0.40	0.10–9.80	11.5–66.3	0–3.50
Taupo	6	42.0–⩾120	Never detected	0.10–0.50	1.0–1.52	0–0.14
Tutaeinanga	4	⩾120	11.10–178	17.03–71.85	37.3–119.0	0–2.09
Ngahewa	2	3.6–4.3	16.22–23.66	1.98–2.64	72.0–159.0	27.63–44.00
Ngahewa	3	⩾120	16.79–54.00	14.05–67.00	31.9–154.0	0.69–5.34
Okaro	8	1.8–30.3	0.00–0.81	0.66–2.77	3.55–32.3	1.14–29.00
Okaro	1	⩾120	2.30	4.00	40.4	0.92
Rerewhakaaitu	5	1.4–4.3	0.00–0.25	0.35–2.51	4.9–25.7	10.50–83.67

partitioned into three size fractions, phosphorus uptake is different for each fraction and varies within fractions depending upon phosphate spike size. This invalidates the basic premise of the radiobioassay and Lean concluded that estimation of ambient orthophosphate by this method is inappropriate for the mixed communities of bacteria and algae that occur in lake water.

Our conclusion is that refinement of technology which combines gel chromatography and molybdenum blue analysis on a continuous flow basis offers the best prospect of assessing orthophosphate in lake waters. Effort will be directed towards establishing the extent to which low molecular weight phosphorus material (PO_4-P) from chromatographs equates with orthophosphate.

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DOWNES, M. T. 1978. An automated determination of low reactive phosphorus concentrations in natural waters in the presence of arsenic, silicon and mercuric chloride. Water Res. 12: 743–745.

DOWNES, M. T., AND H. W. PAERL. 1978. Separation of two dissolved reactive phosphorus fractions in lakewater. J. Fish. Res. Board Can. 35: 1636–1639.

JOHNSON, D. L. 1971. Simultaneous determination of arsenate and phosphate in natural waters. Environ. Sci. Technol. 5: 411–414.

KUENZLER, E. J., AND B. H. KETCHUM. 1962. Rate of phosphorus uptake by *Phaeodactylum tricornutum*. Biol. Bull. Woods Hole 123: 134–145.

LEAN, D. R. S. 1973. Movements of phosphorus between its biologically important forms in lake water. J. Fish. Res. Board Can. 30: 1525–1536.

1981. Partitioning of phosphate uptake by different size classes of lake plankton: implications for the phosphate radiobioassay. Limnol. Oceanogr. (In press)

LEVINE, S. N., AND D. W. SCHINDLER. 1980. Radiochemical analysis of orthophosphate concentrations and seasonal changes in the flux of orthophosphate to seston in two Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 479–487.

PAERL, H. W., AND M. T. DOWNES. 1978. Biological availability of low versus high molecular weight reactive phosphorus. J. Fish. Res. Board Can. 35: 1639–1643.

RIGLER, F. H. 1964. The phosphorus fractions and the turnover times of inorganic phosphorus in different types of lakes. Limnol. Oceanogr. 9: 511–518.

1966. Radiobiological analysis of inorganic phosphorus

in lakewater. Int. Ver. Theor. Angew. Limnol. Verh. 16: 465–470.

1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures orthophosphate in lake water. Limnol. Oceanogr. 13: 7–13.

STAINTON, M. P. 1980. Errors in molybdenum blue methods for determining orthophosphate in freshwater. Can. J. Fish. Aquat. Sci. 37: 472–478.

VAN SCHOUWENBURG, J. A., AND I. WALINGA. 1967. The rapid determination of phosphorus in presence of arsenic, silicon and germanium. Anal. Chim. Acta 37: 271–274.

WHITE, E., AND G. PAYNE. 1980. Distribution and biological availability of reactive high molecular weight phosphorus in natural waters in New Zealand. Can. J. Fish. Aquat. Sci. 37: 664–669.

Competition Between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for Positions in a Michigan Stream[1]

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FAUSCH, K. D., AND R. J. WHITE. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220 – 1227.

Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo truttta*) was studied by measuring characteristics of daytime positions held by brook trout before and after removal of the brown trout from 1800 m of a stream. We used four criteria as indices of position quality: "water velocity difference" (the difference between velocity at the focal point and in the fastest current within 60 cm of the fish), water depth, distance to stream bed, and lighting. After brown trout removal, brook trout larger than 15 cm chose resting positions with more favorable water velocity characteristics and more often in shade. The position shift was greatest for the largest brook trout, those of 20–30 cm. Feeding positions of brook trout changed little upon brown trout removal according to our criteria. The shift in resting positions of brook trout after release from competition with brown trout indicates that brown trout excluded brook trout from preferred resting positions, a critical and scarce resource. The combined effects of such interspecific competition, differential susceptibility to angling, differential response to environmental factors, and predation of brown trout on juvenile brook trout may account for declines of brook trout populations while brown trout populations expand in many streams of the northeastern United States where the two species are sympatric.

Key words: brook trout, brown trout, competition, ecological release, microhabitat use, resting positions, feeding positions, stream, Michigan

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La compétition entre l'omble de fontaine (*Salvelinus fontinalis*) et la truite brune (*Salmo trutta*) a été étudiée par des mesures de caractéristiques des endroits occupés de jour par l'omble de fontaine avant et après l'enlèvement de la truite brune d'une portion de 1800 m d'un cours d'eau. Quatre critères ont été utilisés comme indices de qualité de position : "différence de vélocité de l'eau," (soit la différence entre la vélocité au point focal et au point de courant maximal en dedans de 60 cm du poisson), profondeur de l'eau, distance au lit du cours d'eau et éclairage. Après l'enlèvement des truites brunes, les ombles de fontaine de plus de 15 cm de long choisirent des endroits de repos avec caractéristiques de vélocité d'eau plus favorables et plus souvent à l'ombre. Le changement d'endroit a été le plus prononcé chez les grands ombles de fontaines, ceux de 20–30 cm. Les ombles de fontaine changèrent très peu d'endroit d'alimentation, selon nos critères, après l'enlèvement des truites brunes. Cette modification des endroits de repos de l'omble de fontaine après être libéré de la compétition de la truite brune indique cette dernière excluait les ombles de fontaine de leur endroit de repos préféré, une ressource critique et rare. Les effets combinés d'une compétition interspécifique de cette nature, d'une susceptibilité différentielle à la capture, d'une réponse différentielle à des facteurs ambiants et de la prédation de la truite brune sur les jeunes ombles de fontaine peuvent expliquer le déclin des populations de ces derniers, alors que celles de truites brunes

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prennent de l'expansion dans plusieurs cours d'eau du nord-est des États-Unis où les deux espèces sont sympatriques.

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POPULATIONS of brook trout (*Salvelinus fontinalis*) in streams of the northeastern United States have undergone marked changes since 1900. Anglers and fishery biologists generally concede that abundance, growth, and life span of brook trout have declined and the distribution of populations along stream courses has shifted. Concurrently, in many of the same streams brown trout (*Salmo trutta*) numbers have increased and their distribution has expanded. As brook trout populations appear to dwindle, there is concern that introduction and invasion of brown trout may be a major cause of their decline.

Brook and brown trout evolved separately. Brook trout were indigenous to eastern Canada and the northeastern United States (MacCrimmon and Campbell 1969) but in Michigan only to its upper peninsula (Smedley 1938; Westerman 1974). They were stocked in streams of Michigan's lower peninsula as populations of the now extinct Michigan grayling (*Thymallus tricolor*) declined. Brown trout were introduced from Europe to New York and Michigan beginning in 1883 (MacCrimmon and Marshall 1968). Growth of brook trout first introduced into Michigan's Au Sable River in 1885 declined markedly after brown trout were added in 1891 (Smedley 1938).

In northeastern United States streams where brown trout were introduced or have invaded, brook trout tend now to be more abundant in headwaters and brown trout more abundant downstream. There is often a long zone where populations of the two species overlap, but in many streams brown trout gradually encroach farther upstream each year. This distributional pattern may be due to (1) changes in physical characteristics along the stream course (Gard and Flittner 1974), (2) differential effects of angling, owing to greater catchability of brook trout (Cooper 1952), (3) predation by large brown trout on small brook trout (Alexander 1977), and (4) competition between the two species (Nyman 1970).

The purpose of this study was to examine interspecific competition of adult brook and brown trout for stream positions. Interspecific competition may be defined as the demand by two or more species for a resource in short supply, and requisites for its study are (1) identification of the resources involved and (2) a method to measure competition for these resources.

Previous research indicates that salmonids compete for stream positions that maximize their chances for survival and growth. Kalleberg (1958) proposed that the aggressive defense of territories by salmonids evolved as a mechanism for efficient use of the food supply. Stream salmonids maintain relatively fixed positions with respect to the stream bed, termed focal points, and make short forays from them to feed on invertebrates drifting nearby. Chapman (1966) suggested that competition for space has been substituted for competition for food among stream salmonids. He hypothesized that territory size is linked to food supply as a mechanism to regulate population density. Slaney and Northcote (1974) tested this relationship and found that both salmonid aggression and territory size increased as abundance of drifting prey was reduced. These investigations indicate that space is a critical resource for which stream salmonids compete.

However, because space is linked to food supply, a stream salmonid should compete not just for a certain amount of space but also for an advantageous position offering the best opportunity for securing food and, ultimately, for growth and survival. To achieve this, the fish should maintain positions in slowly flowing water to minimize energy expenditure, but near fast currents carrying more food per unit time to maximize energy intake. Salmonids in Pacific Northwest streams are reported to use positions with these water velocity characteristics (Chapman and Bjornn 1969; Everest and Chapman 1972; Griffith 1972).

"Water velocity difference" is the term Fausch (1978) used to denote the difference between water velocity at the focal point and velocity of the strongest current occurring within 60 cm of the focal point. We assume that positions with the greatest water velocity difference are most advantageous and we use magnitude of velocity difference as the principal criterion of trout position quality. Because we suspect choice of advantageous positions by trout involves not only water velocity and food supply, but also physical structure of the channel and lighting, we also examine other position characteristics.

Because brook and brown trout evolved in similar environments, it is not surprising that they appear to use similar resources. In theory, when similar species occur in sympatry, the competitively subordinate species shifts its use of resources to reduce niche overlap with the dominant (Morse 1974). Nilsson's (1967) review revealed that niche shifts are common among fishes, especially salmonids, and he called the reduction in niche breadth with addition of a species interactive segregation. Conversely, when the dominant species is removed, the subordinate should shift to use more of the preferred resources, a phenomenon termed ecological release.

The ecological release by brook trout to more advantageous positions after removal of the brown trout was our basis for judging whether brown trout dominated and excluded brook trout from preferred positions. Our objective was to compare brook trout position characteristics before and after brown trout removal, using water velocity difference and other measures.

Study Area and Stream Conditions

The study area of the East Branch of the Au Sable River has a low gradient (1 m/km) typical of streams in the glacial deposits of Michigan's northern lower peninsula. It consisted of 1800 m of stream measured upstream from the south edge of Sec. 14, T27N, R3W (44°43′41″N, 84°38′36″W). Here the stream was third order (Strahler system) and averaged 7.5 m

wide and 60 cm deep. The channel bed was sand and gravel with only two pools deeper than 100 cm. The discharge is stable, with mean summer base flow of 1.07 m^3/s (37.7 cfs) at the U.S. Geological Survey gaging station 13 km below the study area, and a 10-to-90% duration discharge ratio of 1.53 (Hendrickson et al. 1973). During the study, discharge at the U.S.G.S. gage ranged from 0.85 to 0.99 m^3/s (30.0–35.0 cfs), about one standard deviation below the 1959–73 mean for July–August, indicating that the study occurred during summer base flow.

The macrophyte *Valisneria americana* was abundant along the silted stream margin in water less than 30 cm deep. Resident fishes included brook and brown trout, slimy and mottled sculpin (*Cottus cognatus* and *C. bairdi*), blacknose dace (*Rhinichthys atratulus*), and Johnny darter (*Etheostoma nigrum*). Brook, brown, and rainbow trout (*Salmo gairdneri*) had been stocked in various amounts and locations in the East Branch until 1964. Current deflectors and overhanging bank coverts made of logs had been installed about 1960 and, although deteriorating, still provided most of the instream cover for trout.

Methods

The senior author used a wet suit, mask, and snorkel to observe positions held by adult brook trout in sympatry with brown trout (July 21–23 and August 11, 1977). Then the brown trout were removed by electrofishing and, after 5 d to allow trout behavior and physiology to return to normal, the observations were repeated (August 20–23).

On each day of diving 2–3 h was spent underwater beginning at 8:30 EDT and a similar period beginning at 13:30. The diver progressed upstream, covering a previously undisturbed 100- to 300-m reach each half day. After removing the brown trout, 300 m at the study area's downstream end and 400 m at the upstream end were omitted from observation as a precaution against observing brook trout that might have been affected by brown trout immigrating from adjacent areas.

Changing underwater visibility complicated observation on most days. It was measured by recording the distance at which an object in the stream disappeared from view. Visibility usually decreased from 4 m or more at 8:30 EDT to 2.5 m or less by 16:30. The decrease was probably caused by light reflecting from colloidal-sized particles, and the diurnal cycle suggests a fine $CaCO_3$ precipitate due to increased photosynthesis of aquatic plants.

To measure positions of trout, the diver crawled slowly along the stream bed, investigating all artificial and natural cover large enough to conceal adults. Most trout remained undisturbed when approached within viewing distance from downstream. Upon sighting an adult trout, the diver remained motionless for 1–2 min. During this period he assessed whether the fish had been disturbed and noted the (1) species, (2) type of position (resting or feeding), (3) size-class of the fish, (4) location of the focal point, and (5) distance of the fish's head from the stream bed. Positions of visibly disturbed fish were disregarded. Fish holding positions beneath submerged cover that was 15 cm or closer to the stream bed were judged to be resting. All other fish positions were classed as feeding. These criteria coincided with observed resting and feeding behavior of East Branch trout.

Brook trout were recorded by three size-classes: 15–20 cm, 20–25 cm, and 25–30 cm. To determine the size of a fish, the stream bed features at its snout and tail were noted and the distance between them measured. With practice, lengths of trout were easily judged to the nearest centimetre without the stream bed measurement.

After underwater observation of a fish, the diver placed a marker in the stream bed and measured five position variables at the focal point: (1) water velocity, (2) maximum water velocity within 60 cm, (3) water depth, (4) distance to nearest cover, and (5) light class. Water velocities were measured with midget Bentzel speed tubes, built according to Everest (1967). Nearest cover was defined as the nearest submerged object that could fully conceal the fish from overhead view. Because resting trout were beneath cover, distance to nearest cover for these fish was zero.

Light at the focal point was visually judged according to three classes: direct light, indirect light, and shade. Direct light was where sunlight reached the stream bed. Indirect light included positions illuminated by sunlight reflected from the stream bed or diffused through riparian foliage. Positions in dark shadows beneath submerged cover were classed as shade. All observations were made at times of bright sunlight.

To remove the brown trout population, we electrofished the entire study area three times during 3 consecutive days. Brown trout abundance was estimated by the improved Leslie method (Ricker 1975) and brook trout abundance by the Schaefer modification of the Petersen mark–recapture method (Regier and Robson 1967). The marking and recapture of brook trout were done on the first and last electrofishing runs. Scales were sampled from a wide range of trout sizes for aging.

Because the majority of resting trout used positions beneath three types of submerged objects, deeply undercut banks in the two large pools, natural logs, and man-made log cover devices, the availability of each type was estimated. As indices of cover, we measured the length of logs and undercut banks beneath which a gauge 15 cm high and 9 cm wide would fit, the same criteria used by Wesche (1976) in his cover rating procedure.

We tested for interspecific competition by measuring change in brook trout position characteristics after brown trout were removed. Because we did not identify individual fish, we compared means of brook trout position variables measured in sympatry versus those in allopatry. Because the six variables at any one position (focal point water velocity, maximum water velocity within 60 cm, water depth, distance to stream bed, distance to cover, and light) were not statistically independent, we compared them simultaneously by multivariate analysis. Three position variables were sensitive indicators of changes in brook trout positions and were used in further tests. These were water velocity difference, water depth, and distance to stream bed.

The main comparisons were multivariate pooled T^2-tests (analogous to univariate t-tests) of brook trout positions in sympatry versus those in allopatry. Four separate tests were made for feeding and resting trout of 15–20 cm and 20–30 cm, only one fish of the latter group being in the 25- to 30-cm class. Heterogeneous variance prevented using a multivariate analysis of variance. When there was a significant difference between position variables in sympatry and

allopatry, multivariate confidence intervals of the differences between means of the three variables were constructed to see which contributed most to null hypothesis rejection. All multivariate procedures are described in Kramer (1972).

Frequencies of brook trout positions in the three light classes were compared with expected frequencies using a contingency table. Sympatry was compared with allopatry in separate tests for resting and feeding brook trout of 15–30 cm.

Results and Discussion

Population Estimates

Numbers of brook and brown trout were grossly unequal in all size-classes except 20–25 cm (Fig. 1). Brook trout of 5–20 cm were much more numerous than brown trout of that size group. Only one brook trout over 25 cm was collected but there were 51 brown trout of 25–60 cm. In population estimates for four 400-m sections of the lower 1600 m of the study area, all but the downstream section held four to six 20- to 25-cm brook and brown trout.

Leslie estimates for brown trout were difficult to calculate because fewer fish were caught on the second electrofishing run than on the third. Therefore, in addition to the formal Leslie regression estimate, a maximum estimate was made using only the first and third runs. The two estimates indicated that 95–99% of brown trout over 15 cm had been removed by electrofishing, so the total number of brown trout captured was used as the population estimate.

Only one age-III brook trout was captured. The age distribution of brown trout was less truncated, with many surviving to age III and some to age V. Mean lengths of brook trout at ages 0 through III were 8.9, 15.9, 20.6, and 30.7 cm. Mean lengths of age 0 through V+ brown trout were 8.0, 18.0, 27.1, 34.9, 43.5, and 48.0 cm, respectively.

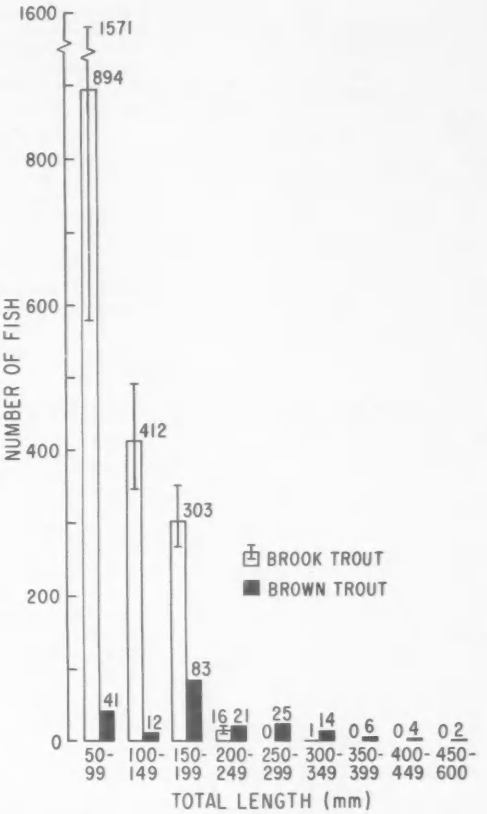

FIG. 1. Length frequency distributions of brook and brown trout in the lower 1600 m of the study area. For brook trout, 95% confidence intervals are indicated. Confidence intervals are not shown for brown trout, as the actual numbers captured were used (see text).

Brook Trout Position Shift

Brook trout held more favorable resting positions after brown trout were removed while feeding positions were relatively unchanged. Resting brook trout of both size-classes, 15–20 cm and 20–30 cm, chose positions with lower mean focal point velocity but greater water velocity difference after brown trout were removed. Water depth and distance to stream bed decreased from sympatry to allopatry for positions of 15- to 20-cm brook trout but increased slightly for the 20- to 30-cm class (Table 1).

Positions held by 15- to 20-cm resting brook trout differed in sympatry and allopatry ($P < 0.10$) but the multivariate confidence intervals (MCI) indicate that most of the difference was due to water depth and some to distance to stream bed (Table 2). Brook trout of 20–30 cm chose resting positions in sympatry that differed significantly from those in allopatry ($P < 0.025$). The MCI show that the difference was mainly due to increase in water velocity difference (Table 2). Resting brook trout of 15–30 cm chose positions with less light more frequently after brown trout were removed ($P < 0.10$). Resting brook trout were found in shade most often and in direct sunlight least often (Fig. 2).

Feeding brook trout chose positions with greater velocity difference and water depth after brown trout removal but these differences were not significant for either the 15- to 20-cm or the 20- to 30-cm size-class ($P >> 0.10$ for both sizes, Table 2). Brook trout of both size-classes fed closer to cover in allopatry but this difference was significant only for 15- to 20-cm fish ($P < 0.01$). Moreover, this position characteristic may be meaningless as trout rarely swam to the nearest cover when intentionally disturbed. Feeding brook trout (15–30 cm) also chose positions with less light more frequently after brown trout removal but the difference was not significant ($P > 0.30$). Brook trout were seen feeding most often in indirectly lit positions, less often in direct sunlight, and never in the shade (Fig. 2).

Evidence for Competition

According to our primary criterion of trout position quality, water velocity difference, adult brook trout occupied more advantageous resting places in the stream after brown trout were removed. In addition, brook trout spent less energy in

TABLE. 1. Characteristics of brook trout positions. Means ± SE are shown for each variable.

Position type	Population type	Sample size (*n*)	Water velocity (cm/s)			Water depth (cm)	Distance (cm)	
			Focal point	Maximum within 60 cm	Difference		To stream bed	To cover
			15- to 20-cm brook trout					
Resting	Sympatry	16	20.4±1.8	36.4±2.3	16.0±1.6	64.7±4.1	3.0±0.5	0.0[a]
	Allopatry	27	12.7±1.8	30.3±2.4	17.6±1.8	51.7±3.2	2.0±0.3	0.0[a]
Feeding	Sympatry	24[b]	26.8±1.6	43.4±2.2	16.6±2.5	66.6±3.7	6.5±0.7	187.3±12.1
	Allopatry	19	24.7±1.5	45.6±1.8	20.9±2.5	72.7±2.3	5.5±0.8	127.9±14.1
			20- to 30-cm brook trout					
Resting	Sympatry	5	19.5±3.0	36.0±3.4	16.5±2.1	61.6±5.6	2.4±0.9	0.0[a]
	Allopatry[c]	3	13.2±3.7	49.8±5.1	36.6±1.8	62.3±3.3	3.0±0.0	0.0[a]
Feeding	Sympatry	5	21.3±3.6	39.0±2.2	17.7±2.2	67.6±4.6	6.8±1.3	172.0±21.3
	Allopatry	5	18.3±2.7	48.8±8.8	30.5±8.8	74.2±5.0	7.0±1.4	134.0±32.2

[a]Resting fish were beneath cover.
[b]One outlier excluded according to the method of Grubbs and Beck described in Gill (1978).
[c]Includes one 25- to 30-cm brook trout.

TABLE. 2. Significance levels of multivariate tests and individual variables.

Comparison	Significance of main tests (*P*)	Significance (*P*) of individual variables		
		Water velocity difference	Water depth	Distance to stream bed
	15- to 20-cm brook trout			
Sympatry vs. allopatry				
Resting fish	<0.10	>>0.10	<0.20[a]	<0.30[a]
Feeding fish	>>0.10			
	20- to 30-cm brook trout			
Sympatry vs. allopatry				
Resting fish	<0.025	= 0.025	>>0.10	>>0.10
Feeding fish	>>0.10			

[a]Because table T^2 values were not available beyond $P = 0.10$, these are conservative estimates of the significance of these variables.

allopatric resting positions because focal point velocities were lower, and occupied more shaded positions after brown trout were removed. This type of ecological release or niche shift resulting from addition or removal of a closely related species is regarded as the strongest and most direct evidence to show interspecific competition for a resource (Diamond 1978; Sale 1979). In contrast, feeding positions of brook trout were similar before and after brown trout removal, indicating little competition for this resource during the study.

Competition can occur only when resources are in short supply. Evidence that resting positions were scarce but that feeding positions were plentiful lies in the hydrology and morphometry of the study area and in our measurements of instream cover.

Because flow in the East Branch is very stable, the trout population should be regulated mainly by the supply of space and food, and not by harsh environmental factors such as floods (Elwood and Waters 1969) and winter ice (Maciolek and Needham 1952). Predation, as well as intra- and interspecific competition for space should adjust the trout population to balance the resource supply (Chapman 1966).

The East Branch channel was wide, shallow, and devoid of trout cover in much of the study area, and there were only two pools with deeply undercut banks. Our cover measurements confirm that trout cover was scarce. In the lower 1600 m of the study area, only 224 m of cover was available to trout, of which 187 m (83%) was formed by man-made cover devices, 28 m (13%) was natural logs, and 9 m (4%) was deeply undercut banks. The mean density of cover was 140 m per stream kilometre. In comparison, a 2400-m study area of the nearby Pigeon River had a mean density of 432 m per stream kilometre of these three cover types (Enk 1977).

Moreover, the East Branch was one standard deviation below base flow during the study, which further limited the amount of resting cover that was submerged. This evidence supports our view that resting positions were in short supply for East Branch trout during the study. Increase in trout populations when permanent bank cover is added to streams also demonstrates that resting positions are a critical resource for stream salmonids in the long term (reviewed by White 1975).

In contrast, feeding positions were abundant in the study area. Trout choose feeding positions beneath principal lines of invertebrate drift but usually with some protection from swift currents (Jenkins 1969). However, channels of rather low

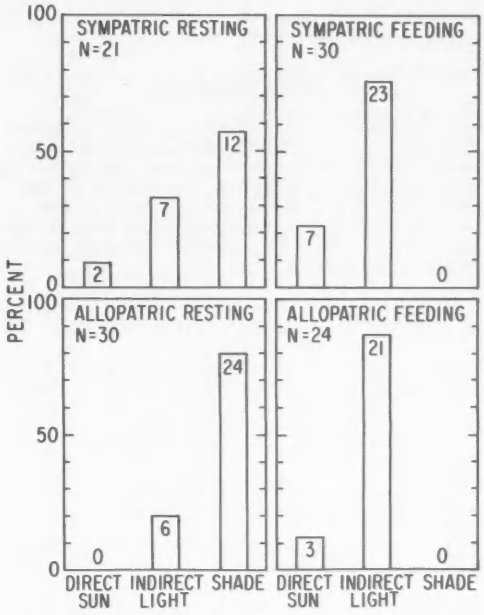

FIG. 2. Use of positions with different lighting by 15- to 30-cm brook trout in sympatry and allopatry. Numbers of observations are shown in bars.

gradient, uniform cross section, and smooth bed, such as the study area, have few refuges from ambient water velocity and lack strong principal currents. Instead, the fairly uniform distribution of water velocities and of invertebrate drift in such channels provides many feeding positions of about equal quality, and little competition for them should be expected. Bassett (1978) studied cover preference of brown trout in artificial channels and proposed that uniform velocity and drift pattern minimized intraspecific competition for feeding positions.

Trout were observed to occupy resting positions during the day unless sufficient invertebrate drift stimulated them to feed. During the study, most drift consisted of *Tricorythodes* mayflies emerging during the morning in late July and early August, and a general emergence of midges (Diptera) and small mayflies (Ephemeroptera) during late afternoon. Brook trout of 20–30 cm moved to daytime feeding positions only when invertebrate drift was far more abundant than that which stimulated 15- to 20-cm brook trout to feed. We assume that large trout fed mainly during late evening when larger stream insects emerged.

Brook trout of both size-classes preferred to feed from indirectly lit positions, using them more frequently after brown trout removal (Fig. 2). Brook trout of 20–30 cm usually held feeding positions in shade beneath instream cover more than 15 cm from the stream bed whereas 15- to 20-cm brook trout often fed in shadows from objects above the water, such as overhanging vegetation. Underwater observations offered an explanation for the use of shade. We speculate that in areas of direct sunlight, the light reflected from suspended particles hampers visibility of trout whereas drift is seen better from shaded positions. Brown trout were seen less often than brook trout, as they were less numerous and chose more concealed resting positions during the day. The seven brown trout observed held positions similar to those used by brook trout of equal sizes.

Our data indicate that resting brook trout held positions closer to swift currents, that is with greater water velocity difference, after brown trout were removed (Table 1). We speculate that trout prefer such resting positions because they allow fish to view organisms drifting nearby and to move to feeding positions quickly in response to increased drift. This visual sampling may be important for efficient foraging.

EFFECT OF BODY SIZE

Although adult brook trout displayed ecological release as predicted, interpretation is hampered because populations of each species were dissimilar in body size distribution (Fig. 1). However, we base most of our conclusions on 20- to 25-cm brook and brown trout, which were nearly equal in number.

Among both juvenile (Newman 1956) and adult salmonids (Jenkins 1969; Bassett 1978) dominance in intraspecific competition is bestowed on individuals of greatest size. Therefore, large brown trout (>30 cm) should have excluded smaller trout of both species from preferred resting positions. Given this, our results might be explained by the alternative hypothesis that the two species are of about equal competitive ability, and that after brown trout were removed, brook trout merely shifted to resting positions previously occupied by the larger brown trout. Had this been the case, however, the smaller brook and brown trout of equal size should have occupied "good" and "poor" resting positions in proportion to their numbers. If we assume that trout resting positions visible to the diver were poorer for survival and growth of trout than concealed positions, then some evidence to refute the "equal competitor" hypothesis is provided by the high ratio of brook to brown trout occupying these poorer (more visible) resting positions.

In the 15- to 20-cm size-class, the ratio of brook to brown trout was 3.65:1 (303:83) in the population but was 8:1 (16:2) in the visible resting positions. The proportion of brook trout observed in these relatively poorer resting positions was greater than the expected proportion found in the population, but not significantly greater ($P = 0.14$) according to a nonparametric test of binomial proportion (Hollander and Wolfe 1973). However, for 20- to 25-cm trout, the ratio of brook to brown trout observed in visible resting positions was 2.5:1 (5:2), significantly greater ($P = 0.07$) than the expected ratio of 0.76:1 (16:21) in the population. Therefore, even though populations were unequal, these results support the view that brown trout were able to exclude equal-sized brook trout from preferred resting positions.

In summary, our data indicate that brook and brown trout competed for preferred resting positions, a critical and scarce resource, and that brown trout were the dominant competitor because brook trout expanded their use of resources to include more advantageous resting positions when released from interspecific competition.

Forces Shaping Sympatric Populations

Dominance of brown trout should be important in changing the relative distribution and abundance of sympatric brook and brown trout populations. However, environmental factors, fishing mortality, and predation may also favor one species in certain situations and thereby effect changes that are difficult to separate from those caused by interspecific competition.

The frequently observed pattern of brook trout in headwaters and brown trout in downstream reaches has commonly been correlated with gradients of water temperature, altitude, stream slope, and stream size (Vincent and Miller 1969; Lane and Skrzynski 1972; Gard and Flittner 1974). However, distribution of the two species cannot be attributed to any one factor because all are related.

Brook trout are more easily caught by fishing than brown trout (Cooper 1952). In a sympatric population exposed to fishing, Marshall and MacCrimmon (1970) found that no brook trout survived to age III but brown trout commonly lived to age V and one fish to age XIII. Similarly, in the East Branch where fishing pressure was moderate, few brook trout lived to age III but brown trout as old as age V were found. In unfished allopatric populations, the oldest brook trout found were age V or VI (Doan 1948; Cooper 1967; O'Connor and Power 1976). Jensen (1971) compared life tables of fished and unfished brook trout populations. In fished populations he found that the balance of birth and death rates was reestablished by drastic changes in age-specific fecundity with selection for early maturity. Male brook trout may be sexually mature as early as age 0 in these populations and females as early as age I. Exploited brown trout populations studied by McFadden and Cooper (1964) showed no such effects.

Predators also kill more brook than brown trout. Alexander (1977) found that adult brown trout ate 4728 and 2219 age-0 brook trout per stream kilometre in two sections of the North Branch of the Au Sable River, Michigan, while eating only 135 young brown trout per kilometre in each section. American mergansers (*Mergus merganser*), belted kingfishers (*Megaceryle alcyon*), great blue herons (*Ardea herodias*), mink (*Mustela vison*), and otter (*Lutra canadensis*) also preyed more heavily on brook trout of all ages than on brown trout (Alexander 1976).

Due to the interaction of competition, predation, fishing mortality, and environmental factors, the mechanisms causing change in sympatric populations remain unclear. However, it is evident that predation and fishing can selectively reduce brook trout populations while brown trout, being more resistant to both forces, typically maintain or increase abundance. Moreover, fishing causes concomitant alterations of brook trout growth and reproduction which reduce the ability of populations to maintain sport fisheries.

We speculate that, as brown trout populations gradually increase, they spread through stream systems to points where they encounter shallowness, undesirably cold or warm temperatures, or other unfavorable conditions. At these limits of distribution, brown trout may be unable to compete successfully with brook trout for space, cover, or food. But in areas where physical conditions are suitable for both species, our results indicate that brown trout can exclude brook trout from preferred resting positions. Gaining these positions should allow brown trout growth and survival to increase at the expense of the brook trout.

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Alexander, G. R. 1976. Diet of vertebrate predators on trout waters in north central lower Michigan. Mich. Dep. Nat. Resour. Fish. Res. Rep. 1839. 18 p.

1977. Consumption of small trout by large predatory brown trout in the North Branch of the Au Sable River, Michigan. Mich. Dep. Nat. Resour. Fish. Res. Rep. 1855. 26 p.

Bassett, C. E. 1978. Effect of cover and social structure on position choice by brown trout (*Salmo trutta*) in a stream. M.S. thesis, Michigan State Univ., East Lansing, MI. 181 p.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. Am. Nat. 100: 345–357.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. p. 153–176. *In* T. G. Northcote [ed.] Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.

Cooper, E. L. 1952. Rate of exploitation of wild eastern brook trout and brown trout populations in the Pigeon River, Otsego County, Michigan. Trans. Am. Fish. Soc. 81: 224–234.

1967. Growth and longevity of brook trout (*Salvelinus fontinalis*) in populations subjected to light exploitation. Trans. Am. Fish. Soc. 96: 383–386.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. Am. Sci. 66: 322–331.

Doan, K. H. 1948. Speckled trout in the lower Nelson River region, Manitoba. Bull. Fish. Res. Board Can. 79. 12 p.

Elwood, J. W., and T. F. Waters. 1969. Effects of floods on food consumption and production rates of a stream brook trout population. Trans. Am. Fish. Soc. 98: 253–262.

Enk, M. D. 1977. Instream overhead bank cover and trout abundance in two Michigan streams. M.S. thesis, Michigan State Univ., East Lansing, MI. 127 p.

Everest, F. H. 1967. Midget Bentzel current speed tube for ecological investigations. Limnol. Oceanogr. 12: 179–180.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board Can. 29: 91–100.

Fausch, K. D. 1978. Competition between brook and brown trout for resting positions in a stream. M.S. thesis, Michigan State Univ., East Lansing, MI. 100 p.

Gard, R., and G. A. Flittner. 1974. Distribution and abundance of fishes in Sagehen Creek, California. J. Wildl. Manage. 39: 347–358.

Gill, J. L. 1978. Design and analysis of experiments in the animal and medical sciences. Vol. I. Iowa State Univ. Press, Ames, IA. 409 p.

Griffith, J. S. Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. J. Fish. Res. Board Can. 29: 265–273.

Hendrickson, G. E., R. L. Knutilla, and C. J. Doonan. 1973. Hydrology and recreation of selected cold-water rivers of the St.

Lawrence River basin in Michigan, New York and Wisconsin. U.S. Geological Survey Water-Resources Investigations 8–73. 73 p.

HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric statistical methods. J. Wiley and Sons, New York, NY. 503 p.

JENKINS, T. M. JR. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behav. Monogr. 2: 56–123.

JENSEN, A. L. 1971. Response of brook trout (*Salvelinus fontinalis*) populations to a fishery. J. Fish. Res. Board Can. 28: 458–460.

KALLEBERG, H. 1958. Observations in a small stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Rep. Inst. Freshwater Res. Drottningholm 39: 55–98.

KRAMER, C. Y. 1972. A first course in methods of multivariate analysis. Virginia Poly. Inst. State Univ., Blacksburg, VA. 351 p.

LANE, E. D., AND W. SKRZYNSKI. 1972. Distribution of native and introduced fishes in the Hinds River system. N.Z. Mar. Dep. Fish. Tech. Rep. 87: 29 p.

MACCRIMMON, H. R., AND J. S. CAMPBELL. 1969. World distribution of brook trout, *Salvelinus fontinalis*. J. Fish. Res. Board Can. 26: 1699–1725.

MACCRIMMON, H. R., AND T. L. MARSHALL. 1968. World distribution of brown trout, *Salmo trutta*. J. Fish. Res. Board Can. 25: 2527–2548.

MACIOLEK, J. A., AND P. R. NEEDHAM. 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. Trans. Am. Fish. Soc. 81: 202–217.

MARSHALL, T. L., AND H. R. MACCRIMMON. 1970. Exploitation of self-sustaining Ontario stream populations of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 27: 1087–1102.

MCFADDEN, J. T., AND E. L. COOPER. 1964. Population dynamics of brown trout in different environments. Physiol. Zool. 37: 355–363.

MORSE, D. H. 1974. Niche breadth as a function of social dominance. Am. Nat. 108: 818–830.

NEWMAN, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. 29: 64–81.

NILSSON, N. A. 1967. Interactive segregation between fish species, p. 295–313. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. J. Wiley and Sons, New York, NY.

NYMAN, O. L. 1970. Ecological interaction of brown trout, *Salmo trutta* L., and brook trout *Salvelinus fontinalis* (Mitchill), in a stream. Can. Field-Nat. 84: 343–350.

O'CONNOR, J. F., AND G. POWER. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek watershed, Quebec. J. Fish. Res. Board Can. 33: 6–18.

REGIER, H. A., AND D. S. ROBSON. 1967. Estimating population number and mortality rates, p. 31–66. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. J. Wiley and Sons, New York, NY.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191. 382 p.

SALE, P. F. 1979. Habitat partitioning and competition in fish communities, p. 323–331. *In* R. H. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

SLANEY, P. A., AND T. G. NORTHCOTE. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory channels. J. Fish. Res. Board Can. 31: 1201–1209.

SMEDLEY, H. H. 1938. Trout of Michigan. Privately published, Muskegon, MI. 49 p.

VINCENT, R. E., AND W. H. MILLER. 1969. Altitudinal distribution of brown trout and other fishes in a headwater tributary of the South Platte River, Colorado. Ecology 50: 464–466.

WESTERMAN. F. A. 1974. On the history of trout planting and fish management in Michigan, p. 15–37. *In* Michigan Fisheries Centennial Rep. 1873–1973. Michigan Dep. Nat. Resour. Fish. Manage. Rep. 6.

WESCHE, T. A. 1976. Development and application of a trout cover rating system for IFN determinations, p. 224–234. J. F. Osborn and C. F. Allman [ed.] Proceedings of the Symposium and Specialty Conference on Instream Flow Needs: Volume II. Am. Fish. Soc., Bethesda, MD.

WHITE, R. J. 1975. In-stream management for wild trout, p. 48–58. *In* W. King [ed.] Wild trout management. Proceedings of the Wild Trout Management Symposium, Trout Unlimited, Denver, CO.

Rainbow Trout (*Salmo gairdneri*) and Cutthroat Trout (*S. clarki*) Interactions in Coastal British Columbia Lakes

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Food, size, and growth of 17 allopatric and 10 sympatric lake populations of rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) were compared as well as their aggressive behavior during feeding in experimental tanks. In allopatry, rainbow trout fed extensively on benthic, midwater, and surface prey. Allopatric cutthroat utilized mostly midwater prey but in contrast with rainbow trout also fish (*Cottus, Gasterosteus*) when available. In sympatry, rainbow trout exploited mainly limnetic surface and midwater prey whereas cutthroat trout utilized more littoral prey and were much more piscivorous in feeding. Allopatric rainbow attained a greater average and maximum size (length, weight) than allopatric cutthroat whereas in sympatric populations cutthroat were clearly larger than rainbow. Growth (size at specific ages) usually was higher for rainbow compared with cutthroat trout in allopatric populations but just the reverse in sympatric populations. When held as matched pairs in aquaria, rainbow consistently were more aggressive than cutthroat trout and displayed different patterns of threat as well as means of prey capture. Differences in feeding and growth in sympatry may result from interactive segregation, the more pronounced aggressiveness of rainbow promoting higher growth in cutthroat trout.

Key words: rainbow trout, cutthroat trout, feeding, growth, habitat, aggressive behavior, feeding behavior, interactive segregation

NILSSON, N.-A., AND T. G. NORTHCOTE. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia lakes. Can. J. Fish. Aquat. Sci. 38: 1228–1246.

Les auteurs ont comparé la nourriture, la taille et la croissance de populations de truites arc-en-ciel (*Salmo gairdneri*) et de truites fardées (*Salmo clarki*) de 17 lacs allopatriques et de 10 sympatriques, en même temps que leur comportement agressif au moment de l'alimentation dans des bassins expérimentaux. En allopatrie, les truites arc-en-ciel se nourrissent abondamment de proies benthiques semi-pélagiques et pélagiques. Les truites fardées allopatriques utilisent surtout des proies semi-pélagiques, mais, contrairement à la truite arc-en-ciel, mangent également des poissons (*Cottus, Gasterosteus*) quand ces derniers sont disponibles. En sympatrie, la truite arc-en-ciel exploite surtout des proies limnétiques de surface et semi-pélagiques, alors que la truite fardée se nourrit principalement de proies littorales et mangent beaucoup plus de poissons. La truite arc-en-ciel allopatrique atteint une taille moyenne et maximale plus grande (longueur, poids) que la truite fardée allopatrique, tandis que dans des populations sympatriques, les truites fardées sont nettement plus grosses que les truites arc-en-ciel. La croissance (taille à des âges spécifiques) est généralement plus forte chez la truite arc-en-ciel que chez la truite fardée dans des populations allopatriques, tandis que c'est le contraire dans le cas de populations sympatriques. Quand des sujets sont appariées en aquarium, la truite arc-en-ciel est toujours plus agressive que la truite fardée et exhibe différentes caractéristiques de menance ainsi que de méthodes de capture des proies. Il se peut que des différences d'alimentation et de croissance en sympatrie résultent d'une ségrégation

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interactive, l'agressivité plus prononcée de la truite arc-en-ciel favorisant une croissance plus forte chez la truite fardée.

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COEXISTENCE and interaction between closely related species of fish has been of increasing interest, especially for Scandinavian and North American fishery biologists, since the early 1950s and the literature has grown immensely in the last few years (for reviews see Nilsson 1967, 1978; Svärdson 1976). These discussions have often dealt with the problem of whether segregation of the species has been of the interactive or the selective type (cf. Brian 1956; Nilsson 1967).

In North America evidence of interactive segregation between salmonids includes that documented between coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*Salmo gairdneri*) (Hartman 1965), coho and cutthroat trout (*Salmo clarki*) (Glova 1978), and cutthroat and Dolly Varden char (*Salvelinus malma*) (Andrusak and Northcote 1971). A study on young coho and chinook salmon (*Oncorhynchus tshawytscha*) by Everest and Chapman (1972) suggested that in this case segregation of the species probably was more of the selective than the interactive type.

Similar relations have been reported in Scandinavia between other "sibling species," for instance Arctic char species (cf. Nilsson and Filipsson 1971; Nyman 1972) and whitefish species (Svärdson 1979).

The study by Hartman and Gill (1968) of rainbow (steelhead) and cutthroat trout distribution in coastal British Columbia rivers has important implications to interaction between these two species. They observed that the rainbow trout "claimed" the large rivers whereas the cutthroat was more abundant in small tributaries or streams with a catchment area of less than 15 km^2. Where the two species were found in the same river the cutthroat was always predominant in the uppermost reaches. In general, their evidence indicated that in streams the rainbow trout was dominant over the cutthroat.

As rainbow and cutthroat trout commonly occur in the same lakes in coastal areas of western North America, the present study was undertaken to compare spatial distribution, feeding, size, and growth between the two species in allopatric as well as sympatric populations.[1] In addition, interactions between the two species during feeding were examined in aquarium experiments.

Materials and Methods

SPATIAL DISTRIBUTION

Information on vertical and horizontal distribution of the two species was obtained from gillnet catches in several of the lakes containing allopatric or sympatric populations. These observations are reported to describe general features of space utilization by rainbow and cutthroat trout in the study lakes and to compare them with observations of other investigators.

In most cases 3-, 5-, and 10-m-deep monofilament nylon gill nets were used containing panels of 25-, 38-, and 51-mm stretched mesh size as described by Andrusak and Northcote (1971). Additional data came from sunken 1- and 2-m-deep gill nets ranging in mesh size from 38 to 128 mm. Unless specified otherwise, netting data represent catches from overnight sets made between spring and autumn.

FEEDING

Some of the data on food eaten by the two species of trout came from stomach analysis records of the British Columbia Fish and Wildlife Branch (Fisheries Research Division). Many of these had been collected earlier by the junior author. Other material came from samples obtained for the study and analyzed using volumetric methods referred to by Andrusak and Northcote (1971) and Nilsson (1955). To simplify sample treatment and to utilize data available from as many populations as possible we have lumped prey identified into four major categories, viz. benthic, midwater, and surface invertebrates, and fish. In some cases more detailed analyses are presented.

GROWTH

Fork length and weight of most fish were measured in the field using spring or beam balances for samples collected up to 1970. Thereafter measurements usually were made in the laboratory on specimens within a few hours of capture using Mettler balances. Age determinations given in Fish and Wildlife Branch records had been made on early collections by several workers using common scale-reading techniques. Fortunately, scale samples were still available for many of these collections so it was possible to check and standardize readings in these cases. Reasonable consistency was found between early and more recent readings on scales from the same fish.

Length/weight and length/age regression statistics were calculated with a computer program available at the University of British Columbia (UBC) Computer Centre.

BEHAVIORAL INTERACTIONS

To compare interactive behavior between rainbow and cutthroat trout, we made observations in summer on paired adults from allopatric stocks of each species held in large tanks with conditions similar to those used by Schutz and Northcote (1972). The experimental fish originated from two wild stocks, the rainbow trout from Jacobs (Marion) Lake and the cutthroat trout from Loon Lake, both in the UBC Research Forest (Table 1). Fish were in separate tanks prior to experi-

[1]In this paper sympatry refers to the coexistence of rainbow and cutthroat trout in the same lake, with or without other fish species; allopatry refers to the existence of these two species in separate lakes, with or without other fish species.

TABLE 1. General characteristics of coastal British Columbia study lakes containing allopatric or sympatric populations of rainbow or cutthroat trout.

Type	Species	Lake	Latitude	Longitude	Elevation, m	Surface area, ha	Max. depth, m	Mean depth, m	Total dissolved solids, mg/L	Other fish species[a]					
										O	KO	DV	3S	PC	PS
					Allopatric										
"Pure"	Rainbow	Garibaldi	49°56′	123°2′	1468	994.3	259	120.7	14	√					
		Healy	49°7′	124°18′	527	33.8	5	1.4	27	√					
		Lightning 1	49°3′	120°50′	1243	26.3	9	4.6	69	√					
		Weaver	49°21′	121°48′	221	82.2	30	12.5	40	√					
"Mixed"	Rainbow	Jacobs (Marion)	49°18′	122°32′	305	13.3	7	2.4	14		√		√		
"Pure"	Cutthroat	Cusheon	48°49′	123°28′	91	26.9	9	4.3	65	√					
		Eunice	49°20′	122°33′	480	18.2	42	15.8	16	√					
		Gooseneck	49°57′	125°31′	300	78.0	38	9.8	40	√					
		Placid	49°19′	122°34′	510	1.6	7	4.3	20	√					
		Twin	50°10′	125°30′	250	27.9	18	4.6	35	√					
"Mixed"	Cutthroat	Loon	49°18′	122°35′	340	48.6	62	27.5	32			√			
	+	Lost	49°19′	122°36′	354	0.6	15	6.0	33			√			
	others	Mike	49°16′	122°32′	229	4.2	6	3.4	32				√		
	(no rainbow)	Oliver	54°17′	130°16′	76	3.0	1.5	0.9	47			√			
		Phyllis	49°34′	123°10′	488	5.2	15	7.9	11			√			
		Rainbow	54°13′	130°5′	30	244.0	20	7.3	4			√	√		
		Ruby	49°44′	124°0′	23	466.2	112	35.7	40		√		√	√	√
					Sympatric										
"Pure"	Rainbow	Drum	49°50′	125°52′	311	20.2	24	10.3	30	√					
	+														
	cutthroat	Elsie	49°27′	125°7′	195	1106.8	21	7.8	32	√					
"Mixed"	Rainbow	Buttle	49°42′	125°34′	221	4203.8	130	70.1	45			√	√		√
	+	Dickson	49°24′	125°5′	200	119.4	16	4.9	25			√			
	cutthroat	Dougan	48°43′	123°37′	30	42.5	13	6.4	112				√		
	+	Fourth Nanaimo	49°4′	124°25′	309	165.5	30	—	30		√	√			
	others	John Hart	50°2′	125°22′	216	362.6	23	12.2	68			√	√		√
		Lower Campbell	50°0′	125°25′	178	2693.6	78	17.1	40			√	√		√
		Lower Clowhom	49°44′	123°31′	30	99.6	16	9.1	<10		√				
		Upper Campbell	49°55′	125°40′	221	2369.8	60	19.2	56			√	√		√

[a]Key to fish species: 0, none; KO, kokanee (*Oncorhynchus nerka*); DV, Dolly Varden (*Salvelinus malma*); 3S, threespine stickleback (*Gasterosteus aculeatus*); PC, peamouth chub (*Mylocheilus caurinus*); PS, prickly sculpin (*Cottus asper*).

TABLE 2. Relative abundance of rainbow and cutthroat trout captured in overnight gillnet sets in study lakes containing sympatric populations of the two species.

Type	Lake	No. of nights fished	Years sampled	Average catch		
				Rainbow	Cutthroat	RB/CT Ratio
"Pure"	Elsie	9	1957, 1960, 1963, 1969	51.8	14.7	3.5[a]
"Mixed"	Buttle	11	1959, 1960, 1963, 1969	56.7	12.8	4.4[a]
	Fourth Nanaimo	2	1954, 1979	17.0	13.5	1.3
	John Hart	1	1951	12	7	1.7
	Lower Campbell	11	1951, 1953, 1957, 1959, 1962, 1963, 1964	23.0	7.5	3.1[a]
	Lower Clowhom	2	1950, 1969	39.0	21.0	1.9[a]
	Upper Campbell	2	1963	46.5	8.5	5.5[a]

[a]Pooled chi-square significant, $P < 0.05$.

ments. Pairs of the same size and species were selected for each test, within an overall fork length range of 20−30 cm. Light conditions (~500 lx at the water surface) and water temperature (about 12−14°C) were held constant during each observation period in the test tanks (122 × 61 × 61 cm). Each pair of fish was held together in the test tank for 5−7 d before observations started.

Interactive behavior of the species pairs was noted for 5-min periods before, during, and after feeding. Three types of aggressive behavior were recorded: lateral threat display, frontal threat display, chasing and nipping as defined by Fabricius (1953), Kalleberg (1958), and Newman (1956, 1960). In total, 778 agonistic acts of rainbow trout and 302 of cutthroat trout were recorded on the 20 intraspecific pairs tested, as well as general features of their feeding behavior and activity. Additional observations were made on 10 interspecific pairs. All tests were conducted during the normal daylight period on fish in the holding tanks.

Description of Study Lakes

Seventeen coastal lakes containing allopatric populations of rainbow or cutthroat trout were used in the study along with 10 lakes with sympatric populations of the same two salmonids (Table 1). Several of the lakes contained "pure" allopatric stocks (i.e. with no other species of fish present) and two had pure sympatric stocks, making the most simple situation in which to examine interactive relationships between rainbow and cutthroat trout. Many of the study lakes had "mixed" allopatric or sympatric stocks (i.e. containing fish species other than rainbow or cutthroat trout), with kokanee (*Oncorhynchus nerka*), Dolly Varden char, threespine stickleback (*Gasterosteus aculeatus*), or prickly sculpin (*Cottus asper*) being common additional members of the fish community.

The lakes ranged geographically from close to the southern end of Vancouver Island (48°43′N, Dougan Lake) to the northern coastal area of the province near Prince Rupert (54°17′N, Oliver Lake) and inland to the summit of the southern coastal mountains (Lightning 1 Lake). Most of the lakes were at elevations less than 500 m but two, Garibaldi and Lightning 1, were over 1000 m (Table 1). Fourteen of the 17 allopatric lakes were relatively small (<100 ha in surface area) and shallow (<16 m in mean depth) whereas several of the sympatric lakes were larger and deeper. Characteristic of most coastal lakes in British Columbia (Northcote and Larkin 1956), their surface waters were low in total dissolved solids, only Dougan Lake being more than 70 mg/L. All of the lakes except the latter lie within the coast and insular mountains limnological region described by Northcote and Larkin (1963). Several of the lakes are in the UBC Research Forest (Eunice, Placid, Jacobs, Loon, Lost) and additional limnological characteristics of these are given by Northcote and Clarotto (1975). McMynn and Larkin (1953) provide details on lakes in the Campbell River system (John Hart, Lower and Upper Campbell, Buttle), all of which have been affected by hydroelectric dams (Sinclair 1965) as have Elsie, Fourth Nanaimo, and Lower Clowhom lakes.

Results

SPATIAL DISTRIBUTION

Allopatric populations — Catches of rainbow trout in gillnet sets made in Garibaldi and Weaver lakes suggested that subadult and adult trout there utilized depths down to at least 10 m and were common in both littoral and limnetic regions of the lakes. In Jacobs Lake, allopatric rainbow trout were most frequently observed in shallow, onshore areas (1−2 m) during early summer, but later (July−August) were found with about the same frequency in deeper (3−4 m) offshore areas as in the onshore ones (Hyatt 1980).

Good evidence for allopatric cutthroat trout having a broad spatial utilization (littoral and limnetic; near surface and near bottom) from summer to autumn in Placid Lake has been presented (Andrusak and Northcote 1971; Shepherd 1973). The introduced allopatric population of cutthroat trout in Eunice Lake (Northcote et al. 1978) utilized the 5-m nearshore zone at all depths from surface to bottom although in offshore waters at 10 m there usually was a preponderance of cutthroat in the uppermost 5-m stratum (Hume 1978; T. G. Northcote, University of Britsh Columbia unpublished data 1979).

In Loon Lake the allopatric cutthroat trout population (cohabiting with Dolly Varden) occupied onshore waters and offshore regions at depths down to at least 10 m (Hume

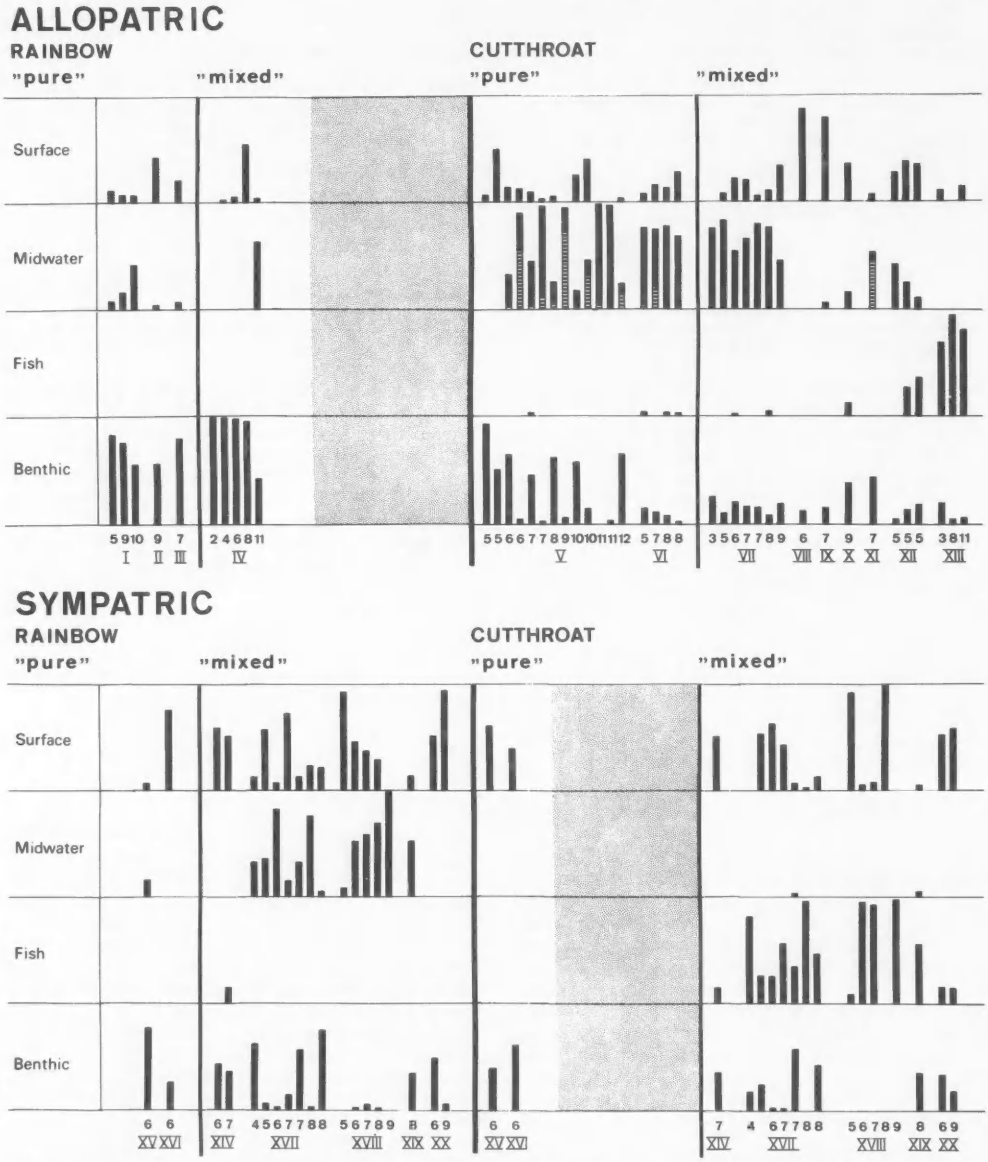

FIG. 1. Major prey categories of allopatric and sympatric rainbow and cutthroat trout in the study lakes; total height for each prey category equals 100% average volume of stomach contents. Arabic numerals indicate months; Roman numerals indicate the lakes sampled as follows: I, Weaver; II, Garibaldi; III, Lightning 1; IV, Jacobs (data from Efford and Tsumura 1973); V, Placid; VI, Eunice; VII, Loon; VIII, Phyllis; IX, Oliver; X, Lost; XI, Rainbow; XII, Mike; XIII, Ruby; XIV, Fourth Nanaimo; XV, Elsie; XVI, John Hart; XVII, Buttle; XVIII, Lower Campbell; XIX, Upper Campbell;XX, Lower Clowhom. Data for Mike Lake in May separated to show prey proportions taken by small, medium, and large cutthroat, left to right; striped bars indicate *Chaoborus*.

TABLE 3. Probable capture site and contribution (average percent stomach volume) of prey taken by allopatric trout populations in two selected study lakes.

Prey site	Prey taxa	Rainbow trout Weaver Lake		Cutthroat trout Loon Lake
		April 19, 1969	October 31, 1978	June 1969
Near surface	Aphididae	3.7		
	Formicidae	1.2		
	Corixa	8.0		
	Lepidoptera			0.3
	Coleoptera	2.0		3.7
	Hymenoptera			1.1
	Tipulidae			0.8
	Chironomidae	0.4	0.4	4.9
	Terrestrial insects[a]	0.4	1.6	13.6
	Hydrachnidae			0.2
	Subtotal	15.7	2.0	24.6
Midwater	*Polyphemus*	6.4		
	Daphnia	7.5	30.9	26.1
	Holopedium	2.6		0.7
	Cladocera[a]		7.3	
	Diaptomus		<0.1	27.5
	Chaoborus		1.8	
	Subtotal	16.5	40.0	54.3
Near bottom	Hirudinea		3.0	
	Hyalella	4.3	10.3	0.6
	Amphipoda[a]	0.9		
	Ephemeroptera	1.3	2.2	0.4
	Plecoptera		0.3	
	Sialis		5.7	1.0
	Odonata		2.9	3.1
	Trichoptera	26.8	10.0	1.6
	Hydrophorus	0.4		
	Chironomidae	10.4	18.9	7.1
	Diptera[a]			4.8
	Aquatic insects[a]	23.4		
	Planorbidae		4.4	
	Sphaeriidae		0.3	
	Mollusca[a]	0.2		
	Subtotal	67.7	58.0	18.6
Variable	Fish[a]			0.9
	Subtotal	0	0	0.9
Unknown	Debris[a]	0.1		1.6
	Number with food	23	35	80

[a]Unidentified.

1978). During spring and summer, however, numbers in offshore areas were usually much lower in the 5- to 10-m depth stratum than in the 0- to 5-m stratum. Similar spatial distributions of allopatric cutthroat have been noted in several other coastal B.C. lakes including Phyllis (Andrusak and Northcote 1970) where they cohabit with Dolly Varden.

Sympatric populations — In Elsie Lake adult rainbow trout were silvery and small, rarely exceeding 25 cm in length, and most abundant in limnetic regions down to depths of 5–6 m. Adult cutthroat trout, on the other hand, frequently attained lengths over 70 cm and particularly the largest individuals were commonly taken in littoral regions of the lake. Similarly in Lower Clowhom Lake, catches suggested that rainbow were more pelagic in distribution than cutthroat trout, which were most frequently captured in shallow, nearshore waters. Spring to autumn gillnet catches (1969) in Buttle Lake also indicated that the rainbow adults were more pelagic in distribution whereas the adult cutthroat foraged near the bottom in littoral areas less than 3 m deep.

RELATIVE ABUNDANCE

Information on relative abundance of rainbow and cutthroat

TABLE 4. Probable capture site and contribution (average percent stomach volume) of prey taken by "pure" sympatric trout in Elsie Lake.

Prey site	Prey taxa	Rainbow trout		Cutthroat trout
		June 1969	August 21, 1969	June 1969
Near surface	Hemiptera	0.7	3.5	0.2
	Hymenoptera	15.3		17.5
	Coleoptera	6.5	2.9	10.7
	Corrodentia	0.8		
	Diptera	3.3		
	Terrestrial insects[a]	12.3	5.9	
	Araneae	0.8		0.5
	Subtotal	39.7	12.3	28.9
Midwater	*Polyphemus*		4.7	
	Daphnia		3.5	
	Diaptomus		5.6	
	Zooplankton[a]		2.4	
	Subtotal	0	16.2	0
Near bottom	*Hyalella*	0.8	4.3	
	Asellus		0.8	
	Corixa		0.5	
	Ephemeroptera	1.3	9.7	
	Plecoptera			0.2
	Sialis			0.2
	Trichoptera	1.4	27.1	4.9
	Chironomidae	47.2	6.2	48.7
	Aquatic insects[a]	9.2	16.8	
	Lymnaea			3.9
	Mollusca[a]		4.7	
	Salamander			4.4
	Subtotal	59.9	70.1	62.3
Unknown	Debris[a]	0.4	1.4	8.8
	Number with food	58	17	19

[a]Unidentified.

trout was available from overnight sets made with floating and sunken gill nets in 7 of the 10 study lakes containing sympatric populations. Although no attempt was made to set the nets in locations or positions which would select for one or the other species, because most were placed close to shore rather than in midlake sites, probably selection for cutthroat trout, if any, would have been favored. Results from 38 separate sets in the study lakes (Table 2) indicated that in all lakes more rainbow than cutthroat were captured in the sets. Average catch ratios in favor of rainbow trout ranged from 1.3 to 5.5 and pooled chi-square analysis showed that the proportions of the two species captured were significantly different in all lakes except Fourth Nanaimo and John Hart.

FEEDING

Most fishes of arctic and temperate areas are opportunistic in their feeding habits so small samples only reflect the diet of the fish a few hours prior to their capture. We think that by gathering samples from several lakes at different seasons and years, we have obtained a broad sampling and hence a good generalized picture of the food niches of rainbow and cutthroat trout in allopatric and sympatric situations.

Allopatric populations — Samples of rainbow trout were taken from Weaver, Garibaldi, Lightning 1, and Jacobs lakes (Fig. 1, I–IV). Jacobs Lake also contains kokanee, which might imply that the two species compete for plankton. The preference for benthic food both in pure and mixed situations is, however, obvious (Fig. 1). As a good example of the variety of this food category the material from Weaver Lake has been chosen (Table 3). Chironomid larvae as well as Trichoptera larvae were predominant as food both in spring (April) and autumn (October). In addition, however, consumption of crustacean plankton, especially in the autumn (*Daphnia rosea*), was considerable. The samples from the other lakes in question on the whole support this general picture (Fig. 1). No fish at all was found in the stomach analyses, not even in Jacobs Lake, where kokanee is a common fish species. As compared with cutthroat trout the rainbow tend to feed more extensively on benthic prey, less on midwater prey, and above all show no affinity to predation on fish, in these lakes at least.

We should note, however, that the only "mixed" situation presented here is Jacobs Lake, where the rainbow coexist with kokanee. In many interior B.C. lakes allopatric rainbow trout living with other fishes display a very pronounced piscivorous habit, for example, in Paul Lake (Crossman 1959; Johannes and Larkin 1961), where large rainbow prey on redside shiner (*Richardsonius balteatus*) and in Kootenay Lake where they

TABLE 5. Probable capture site and contribution (average percent stomach volume) of prey taken by "mixed" sympatric trout in Buttle Lake, 1969.

Prey site	Prey taxa	Rainbow trout			Cutthroat trout		
		April 23	July 15	August 5	April 23	July 15	August 5
Near surface	Hemiptera		0.1	3.2			
	Megaloptera			0.7			
	Trichoptera			2.8			3.3
	Coleoptera	7.7	7.9	4.3		6.1	1.0
	Hymenoptera		0.6	0.9			2.2
	Lepidoptera		2.4				
	Diptera[a]	20.0		4.5			
	Chironomidae						0.2
	Empididae		0.3	2.4			0.3
	Formicidae		0.1	0.8			
	Araneae	1.9		0.8			
	Terrestrial insects[a]		2.0	3.0			4.4
	Subtotal	29.6	13.4	23.4	0	6.1	11.4
Midwater	*Holopedium*			3.9			
	Diaptomus		21.1				
	Subtotal	0	21.1	3.9	0	0	0
Near bottom	Hirundinea						0.5
	Corixa		0.2				
	Ephemeroptera	2.7	46.0	50.0	3.4	17.1	1.2
	Trichoptera	33.4	10.9	17.6	11.5	23.6	23.4
	Plecoptera		0.4	0.6	0.1		6.7
	Dytiscidae			1.1			1.3
	Chironomidae	16.7	4.0	3.4	0.1	6.7	1.6
	Ceratopogonidae						0.7
	Blepharoceridae		0.3				
	Simulidae		0.6				
	Aquatic insects[a]						7.3
	Subtotal	52.8	62.4	72.7	15.1	47.4	42.7
Variable	Frog (tadpole)					6.7	
	Fish (*Cottus asper*)	7.7					
	(*Gasterosteus aculeatus*)				}81.5[b]	}30.3[b]	}44.4[b]
	Subtotal	7.7	0	0	81.5	37.0	44.4
Unknown	Debris[a]	9.9	3.1		3.4	9.5	1.5
	Number with food	13	41	32	39	15	15

[a]Unidentified.

[b]Brackets indicate that cutthroat trout stomachs on these dates contained both *Cottus asper* and *Gasterosteus aculeatus* jointly contributing the amount indicated. Rainbow trout stomachs on April 23 contained only *Cottus asper* in the fish category.

prey heavily on kokanee (Northcote 1973).

Samples of cutthroat trout were taken from nine lakes, viz. Placid, Eunice, Loon, Phyllis, Oliver, Lost, Rainbow, Mike,and Ruby lakes (Fig. 1, V–XIII). In all lakes except Eunice the populations are native. In Eunice Lake, which was originally fishless, cutthroat were first introduced in the autumn of 1974 (Northcote et al. 1978).

Obviously midwater prey (crustacean plankton and *Chaoborus*) are the main items consumed by the cutthroat, except in Mike Lake, where surface prey (mainly terrestrial insects) and fish (mainly threespine stickleback) are important (see Fig. 1). Still more extensive feeding on fish was displayed by Ruby Lake cutthroat in March–November 1970. There the average consumption of stickleback, peamouth chub (*Mylocheilus caurinus*), and kokanee ranged between 70 and 95.7% (the proportion between stickleback and peamouth chub being about 10:1). The importance of benthic prey and fish obviously increases with the age and size of the fish (see Mike Lake).

In Eunice Lake (VI), the cutthroat in the first 2 yr after introduction virtually eliminated the midwater *Chaoborus* population and utilized other midwater prey. Nevertheless, surface and benthic prey formed a greater portion of their diet than in the allopatric Loon Lake population (Hume 1978).

Compared with allopatric rainbow trout, cutthroat tend to feed more extensively on midwater prey and fish (see Loon Lake, Table 3).

Sympatric populations — The most extensive samples of sympatric cutthroat and rainbow came from Buttle and Upper and Lower Campbell lakes on Vancouver Island, and from Lower Clowhom Lake, where kokanee is also present (Fig. 1

TABLE 6. Probable capture site and contribution (average percent stomach volume) of prey taken by "mixed" sympatric trout in Upper and Lower Campbell[a] and Lower Clowhom lakes.

Prey site	Prey taxa	Upper Campbell August 1964		Lower Campbell May–August 1964		Lower Clowhom June 1969	
		Rainbow	Cutthroat	Rainbow	Cutthroat	Rainbow	Cutthroat
Near surface	Hemiptera				2.4		0.6
	Coleoptera	4.4	5.6	0.4	2.4	7.1	8.0
	Hymenoptera	0.8			0.1	26.0	8.3
	Bombus						2.4
	Formicidae				6.8	0.2	3.8
	Isoptera				3.3		
	Diptera			3.6	3.5		
	Chironomidae	2.5					
	Araneae			0.3			0.6
	Terrestrial insects[b]	4.0			5.7	16.8	27.2
	Subtotal	11.7	5.6	4.3	24.2	50.1	50.9
Midwater	*Holopedium*	1.7		0.3			
	Daphnia	25.4		2.1			
	Diaptomus	24.1	4.2				
	Subtotal	51.2	4.2	2.4	0	0	0
Near bottom	Ephemeroptera					0.4	1.9
	Plecoptera					0.1	
	Trichoptera	5.5	8.1	0.2		18.4	9.0
	Dytiscidae		2.2				
	Hydroporus		0.3				
	Chironomidae	27.5	10.3	83.4	36.6	19.1	12.1
	Aquatic insects[b]	1.9	0.5	9.7	3.9	2.7	9.6
	Physaidae		7.0		0.4		
		34.9	28.4	93.3	40.9	40.7	32.6
Variable	Fish[b]						13.7
	Gasterosteus aculeatus						
	Cottus asper		}57.0[c]		}34.6[c]		
	Subtotal	0	57.0	0	34.6	0	13.7
Unknown	Debris[b]	2.2	4.8		0.3	9.2	2.8
	Number with food	30	18	29	29	21	21

[a]Data from Sinclair (1965).
[b]Unidentified.
[c]Brackets indicate that both fish species mentioned jointly contributed the total amount indicated to the average stomach volume; because of the recording system used, it was not possible to separate independent contribution of each species in all cases.

and Tables 4–6).

In sympatry, cutthroat trout were highly piscivorous. Even individuals less than 20 cm in length fed on fish and in most larger ones this prey category usually accounted for 80% or more of the average volume of food taken. No instances of cutthroat definitely having preyed on rainbow trout or its own species were noted.

The rainbow, on the other hand, fed more on crustacean plankton (mainly large *Daphnia*) in sympatry than in allopatry. Only one case of rainbow feeding on fish (a cottid in April 1969, Buttle Lake, Table 5) was recorded.

Surface prey (mainly terrestrial insects) were about equal for rainbow and cutthroat. Different species of Coleoptera and Hymenoptera were on the whole most frequent, but also ants (Formicidae) and termites (Isoptera) at times filled the stomachs of these fish. The most important adult aquatic insect group was by all means the Chironomidae.

On the whole, the two species in sympatry seem to be segregated into different food niches, mainly implying that cutthroat utilize fish (mainly stickleback and sculpins) or surface prey but rarely midwater prey, in sharp contrast with the allopatric situations. The tendency of cutthroat to feed on other fish is more pronounced when in sympatry with rainbow. Rainbow, on the other hand, seem to "take over" the midwater food niche but still retain the surface and benthic food niches, though almost never that of piscivory.

The presence of other species, for instance Dolly Varden char and kokanee, should of course affect the feeding of rainbow and cutthroat, kokanee being a very efficient plankton-feeder and Dolly Varden being mainly a benthofagous species in small coastal lakes at least (Andrusak and Northcote 1971). This holds true especially in lakes cohabited by kokanee. In most cases where this species is present (e.g. Lower Clowhom Lake), it has "taken over" the role of crustacean planktivory and the rainbow turns to other food items.

Several of our large study lakes have been subjected to impoundment for hydroelectric purposes, so that benthic prey probably have been reduced within the littoral zone (e.g.

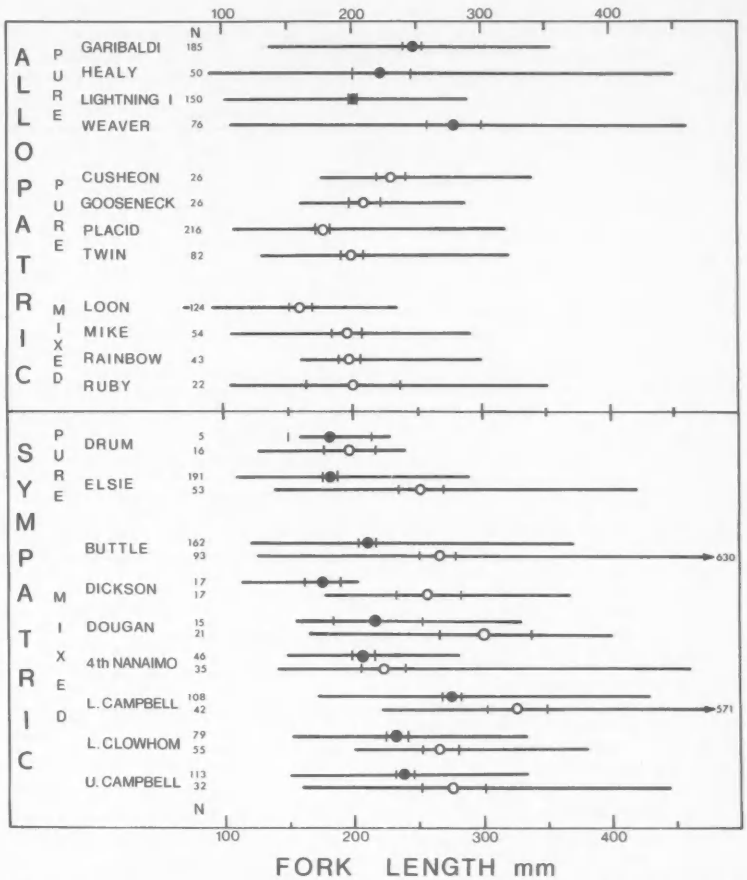

FIG. 2. Length characteristics of allopatric and sympatric populations of rainbow (●) and cutthroat (○) trout from gillnet sets in the study lakes. Averages indicated by solid and open circles, ranges by horizontal lines, 0.95 confidence intervals by short vertical lines, and sample size (*n*) by numbers at left. Data from following years: Garibaldi, 1949, 1950, 1951; Healy, 1970; Lightning 1, 1952; Weaver, 1951, 1978; Cusheon, 1972; Gooseneck, 1956; Placid, 1967, 1969, 1979; Twin, 1978; Loon, 1951, 1974; Mike, 1951, 1958; Rainbow, 1952; Ruby, 1969; Drum, 1956; Elsie, 1969; Fourth Nanaimo, 1951, 1954, 1979; Buttle, 1969; Dickson, 1957; Dougan, 1951; Lower Campbell, 1951, 1959, 1963; Lower Clowhom, 1950, 1969; Upper Campbell, 1951, 1963.

Grimås 1961; Nilsson 1964).

SIZE AND GROWTH CHARACTERISTICS

Although there were considerable differences in limnological features of study lakes containing allopatric trout populations (Table 1), the average lengths of trout captured did not vary greatly (Fig. 2), most being close to 200 mm. In general, average and maximum lengths of the allopatric rainbow caught were greater than most of those in allopatric cutthroat populations, several significantly so. A similar pattern was shown, though less clearly, for average and maximum weights of allopatric trout (Fig. 3).

Quite the opposite trend appeared in sympatric populations. Not only was there much more variation in average and maximum lengths or weights of trout between lakes (Figs. 2, 3), but most cutthroat populations in sympatry showed higher averages than those in allopatry, some even exceeding those for allopatric rainbow. Even of more interest was the clear trend for sympatric cutthroat populations to be larger in average length and greater in average weight than rainbow populations in the same lake. Eight of the nine sympatric populations (Elsie, Fourth Nanaimo, Buttle, Dickson, Dougan, Lower Campbell, Lower Clowhom, and Upper Campbell) all

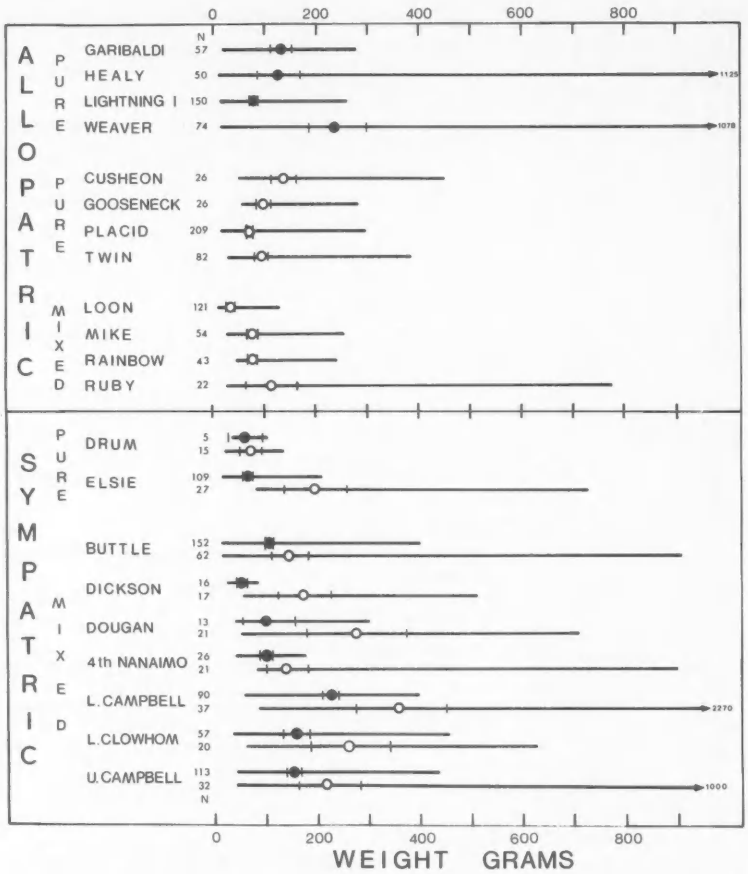

FIG. 3. Weight characteristics of allopatric and sympatric populations of rainbow (●) and cutthroat (○) trout from gillnet sets in the study lakes. Averages indicated by solid and open circles, ranges by horizontal lines, 0.95 confidence intervals by short vertical lines, and sample size (n) by numbers at left. Data from same years as in Fig. 2 with the following exceptions: Garibaldi, 1949, 1950; Placid, 1967, 1979; Elsie, 1951, 1954; Lower Clowhom, 1950.

have cutthroat with average lengths significantly greater than their respective rainbow trout and with much greater maximum lengths for cutthroat compared with rainbow trout (Fig. 2). Average weights of cutthroat are greater than rainbow trout in all sympatric populations, significantly so in at least five cases (Fig. 3).

Length/weight regressions ($\log_{10}$) were plotted for all allopatric and sympatric populations of rainbow and cutthroat trout where sufficient data were available and tested for differences in slope as well as intercept (displacement). No consistent trend was evident in comparisons between pure allopatric populations (Table 7); in 5 of the 12 cases where significant differences appeared, rainbow trout showed higher slopes or intercepts than did cutthroat trout. The two alpine lake stocks of allopatric rainbow trout (Garibaldi and Lightning 1) in most cases showed lower regression slopes or displacement when compared with the allopatric cutthroat trout pure stocks. In comparisons between mixed (cutthroat) allopatric populations, there were far more cases (11 out of 16) where rainbow slopes or intercepts were significantly higher than those for cutthroat trout. Of course, comparisons between populations in different lakes may be affected by poor food production or feeding conditions in particular lakes. The Mike Lake population may be a case in point because its allopatric cutthroat trout showed significantly lower length/weight regressions in all four comparisons with the allopatric rainbow populations (Table 7). That cutthroat from Mike Lake, where stickleback are present and utilized as prey, should be poor in condition (length/weight) when compared with alpine allopatric rainbow in a low productivity lake such as Garibaldi is surprising.

TABLE 7. Matrix for significant ($P < 0.05$) differences in length/weight regression ($\log_{10}$) between allopatric rainbow and cutthroat trout populations.[a]

Type	Cutthroat populations	"Pure" rainbow populations			
		Garibaldi	Healy	Lightning 1	Weaver
"Pure"	Cusheon	CT[b]		CT[b]	
	Gooseneck		RB[b]	CT[c]	CT[c]
	Placid	CT[b]	RB[b]	CT[c]	
	Twin	RB[c]	RB[b]	CT[c]	RB[c]
"Mixed"	Loon	CT[b]	RB[c]	CT[b]	CT[b]
	Mike	RB[b]	RB[b]	RB[b]	RB[b]
	Rainbow	RB[c]	CT[c]	RB[c]	RB[c]
	Ruby	CT[c]	RB[b]	RB[c]	RB[b]

[a]Data from same years as in Fig. 3 with following exceptions: Placid, 1967, 1979; Garibaldi, 1949, 1950.
[b]Species showing significantly higher slope of length/weight regression.
[c]Species showing significantly higher intercept (weight) of length/weight regression.

TABLE 8. Lakes showing significant ($P < 0.05$) differences in length/weight regressions ($\log_{10}$) between their sympatric rainbow and cutthroat trout populations.[a]

Stock type	Population tested	Significant length/weight regression
"Pure"	Drum	
	Elsie 1957	
	Elsie 1969	
"Mixed"	Buttle 1963	
	Buttle 1969	Cutthroat[c]
	Dickson	
	Dougan	
	Fourth Nanaimo	Cutthroat[c]
	Lower Campbell	Cutthroat[c]
	Lower Clowhom	
	Upper Campbell	Rainbow[b]

[a]Unless indicated, data from same years as in Fig. 3 with following exceptions: Fourth Nanaimo, 1951, 1954; Lower Clowhom, 1950.
[b]Species showing significantly higher intercept (weight) of length/weight regression.
[c]Species showing significantly higher slope of length/weight regression.

Significant differences in length/weight regressions between sympatric rainbow and cutthroat trout were only found in four cases (Table 8) and, in two of these, the cutthroat showed significantly higher slope compared with the rainbow.

Growth of the allopatric trout populations was compared in the study lakes by plotting lengths at capture against age (completed years) determined by scale reading (Fig. 4). There were, of course, differences between lakes in growth rate and average size at particular ages for rainbow or cutthroat trout. For example, rainbow from Weaver Lake clearly grew much faster than those in Lightning 1 (average length at ages 2 and 3 significantly higher in Weaver; $P < 0.05$). Likewise, the growth rate of Ruby Lake cutthroat after 2 yr of age was higher than in many other allopatric cutthroat lakes (Fig. 4). Nevertheless, in the allopatric lakes in general, rainbow trout were usually larger than cutthroat trout at ages 2–4. (Fig. 4, Table 9). In 67 of 79 comparisons where data were adequate or available, the average sizes of rainbow at specific ages were larger than for cutthroat trout, and significantly so in 42 out of 44 cases where such differences could be demonstrated.

In sympatric populations there was consistent evidence in nearly all of the stocks, whether pure or mixed, that cutthroat trout attained a larger size at specific ages than did rainbow trout (Fig. 5). Evidence to support this was obtained by comparing differences in average size at ages 2–6 where data were adequate to make statistical comparisons. In 31 out of 32 such cases, the average lengths of cutthroat were greater than rainbow significantly so in 24 cases (Table 10).

Length ($\log_{10}$)/age regressions for allopatric populations showed significant differences in slope or intercept in 25 comparisons of rainbow and cutthroat trout (Table 11). In 16 of these, the rainbow had significantly higher slopes or intercepts. In contrast, for the sympatric populations where significant differences in slope or intercept were found between the two species, in all cases the cutthroat were higher (Table 12).

In sympatry, the cutthroat invariably grew faster than rainbow. When sculpins or sticklebacks were present, this faster growth may have resulted from feeding on them. As cutthroat have a wider gape and more "predatory" dentition, they may be "preadapted" to utilize larger food items than the rainbow.

The presence of other salmonid species should not be forgotten. It has already been stated that kokanee play a large role as an interactor when present, adapted as they are to feeding on plankton. As far as our data are concerned, however, they do not seem to influence the basic feature of cutthroat being fast growing and rainbow slow growing when the two species are in sympatry.

INTERACTION EXPERIMENTS

The experiments on interactive behavior were very simple, aimed only at the question concerned with which of the two species was the most aggressive and in what way the aggression might be displayed in a simple environment with no complicating features other than the addition of light and food. We do not, therefore, claim that the behavior recorded in these experiments was necessarily similar to what happens in a natural lake. Because of logistic difficulties, regular observations could only be made for a 3-wk period in summer.

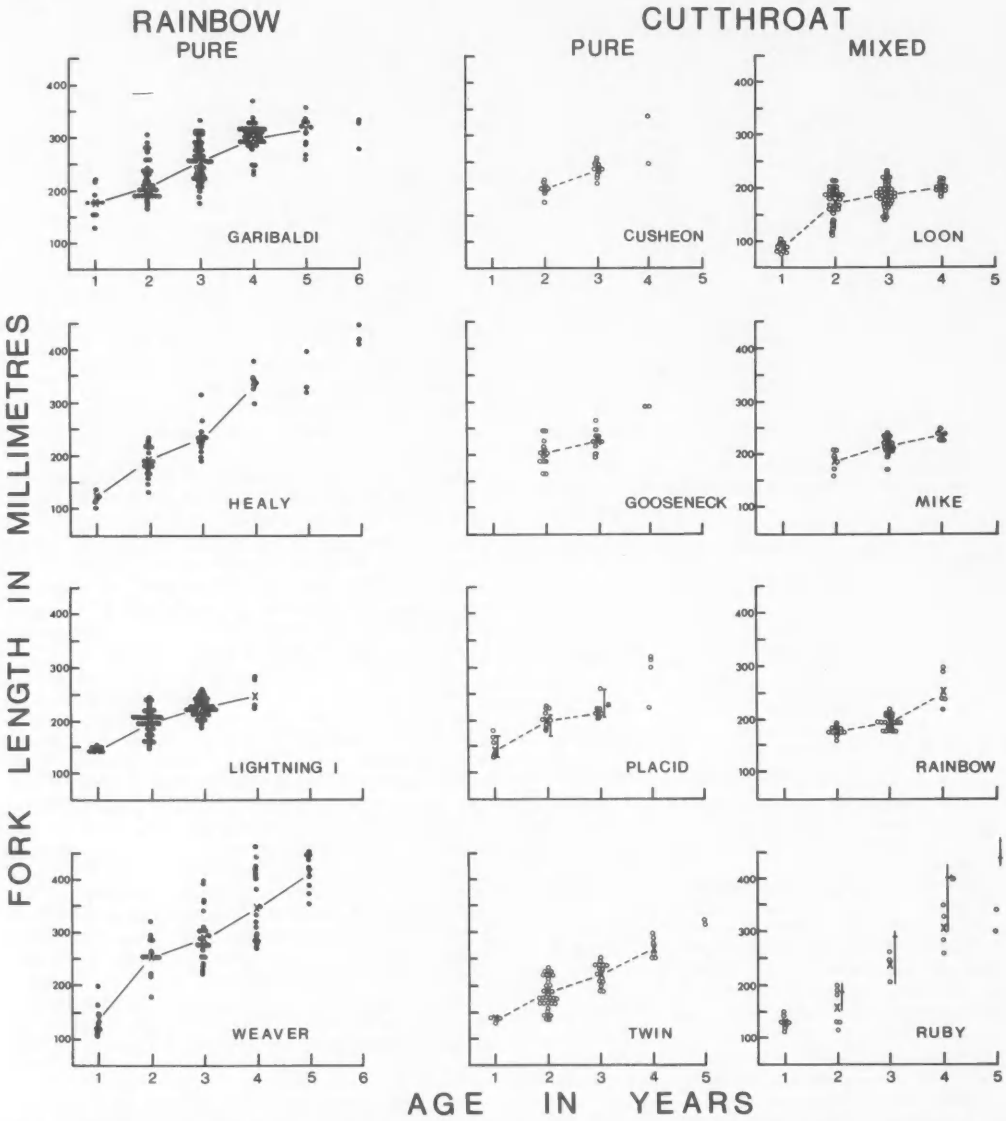

FIG. 4. Growth characteristics of allopatric populations of rainbow (●) and cutthroat (○) trout in the study lakes; averages indicated by ×, rainbow ——, cutthroat ----. a, probable range determined by length/frequency analysis of samples from 1967, 1971 (Shepherd 1973); b, average length and range of 84 fish aged by scale reading (G. D. Taylor data). Data from same years as in Fig. 2 with the following exceptions: Placid, 1969, 1979; Mike 1951.

Paired specimens of either rainbow or cutthroat were held in tanks and intraspecific agonistic activities in connection with feeding were counted. Because of the very vigorous agonistic behavior of the rainbow, quickly killing cutthroat when paired with that species, most of the data obtained consisted of records of rainbow and cutthroat being held with specimens of their own species.

Three types of aggressive behavior were observed: (1) "nipping" and "chasing," i.e. direct fighting, when the dominant fish tried to bite the fins of its competitor or chase

TABLE 9. Matrix for differences in average length at age between allopatric rainbow and cutthroat trout populations. Species with greater average length at each age indicated by symbols (RB, rainbow; CT, cutthroat) and underlined where significant ($P < 0.05$).

Type	Cutthroat populations (same ages)	"Pure" rainbow populations											
		Garibaldi			Healy			Lightning 1			Weaver		
		2	3	4	2	3	4	2	3	4	2	3	4
"Pure"	Cusheon	RB	RB	b	CT	CT	b	CT	CT	b	RB	RB	b
	Gosseneck	RB	RB	b	CT	RB	b	CT	RB	b	RB	RB	b
	Placid	RB	RB	b	CT	RB	b	CT	RB	b	RB	RB	b
	Twin	RB	RB	RB	RB	RB	RB	RB	CT	b	RB	RB	RB
"Mixed"	Loon	RB	RB	RB	RB	RB	RB	RB	RB	b	RB	RB	RB
	Mike	RB	RB	RB	RB	RB	RB	RB	RB	b	RB	RB	RB
	Rainbow	RB	RB	RB	RB	RB	RB	RB	RB	b	RB	RB	RB
	Ruby	RB	RB	CT	RB	CT	RB	RB	CT	b	RB	RB	RB

[a]Data from same years as in Fig. 3 with following exceptions: Placid, 1969, 1979; Mike, 1951.
[b]Sample size inadequate or no data.

it away; (2) "lateral threat display," when the competitors were swimming side by side with fins stretched and the body flexed, as described by Fabricius (1953) and Kalleberg (1958), often accompanied by an oscillation of the body; and (3) "frontal threat display," when the competitors approached each other with arched backs, lowered dorsal fins, and extended gular pouches (cf. Kalleberg 1958; Newman 1960).

Of 778 intraspecific aggression acts (types 1 + 2 + 3) of rainbow and 302 of cutthroat (Fig. 6), rainbow consistently was the most aggressive species and the addition of food increased its aggressive behavior. This is consistent with other observations of fish behavior (e.g. Newman 1960; MacPhee 1961; Magnuson 1962; Nilsson 1963). For cutthroat, little change in aggressiveness was noted during or after feeding compared with that before feeding (Fig. 6). Most of the aggressive acts in both species were chases or nips.

Both species usually took the food ration at or near the surface, as they often do in their natural habitats. The rainbow, however, usually made powerful leaps as soon as the food landed on the surface whereas cutthroat approached the food cautiously and nibbled, with only the nose above the surface.

Although rainbow consistently were more aggressive than cutthroat when being observed in tanks, they also differed in other aspects of behavior. The dominant rainbow, for instance, in the experiments attacked their partners by making rapid rushes and biting. In an attempt to escape, the pursued fish sometimes leapt high out of the water or kept hiding in a corner of the tank without moving or trying to feed. Two rainbow trout of apparently "similar rank" that had recently come into contact mostly threatened each other by lateral displays with vibrating bodies. In this context the color of the fish also changed; that of the dominant fish faded whereas the subdominants took on a darker color. This is in agreement with Newman's observations (1960). No frontal threat displays were ever recorded in rainbow trout pairs.

The cutthroat appeared to be "calmer"; their attacks were carried out more slowly and "deliberately." The subordinate fish appeared to swim away only as far as was necessary. The cutthroat, but never the rainbow, exhibited frontal threat display, lowering the hyoid region so that the red slashes could be seen. This behavior presumably served as a social signal to warn a subordinate individual of the same species (cf. Newman 1960).

When, towards the end of the study, rainbow were released into the same aquarium as cutthroat (10 interspecific pairs), they reacted to each other with the same behavioral repertoire as with individuals of their own species but with different intensity. Invariably, it was the rainbow that dominated cutthroat of the same size. In some cases, it took only a night for a rainbow to "stress to death" a cutthroat that for a couple of months had been dominant over fish of its own species. One large (about 30 cm) cutthroat (Marion Lake stock; Schutz and Northcote 1972), however, did gain dominance over a small (about 20 cm) rainbow trout.

Discussion

Although rainbow and cutthroat trout commonly cohabit in coastal British Columbia lakes, little work has been done to measure relations between these species. This is a first attempt to describe some aspects of interaction between the two closely related species in coastal lakes and to speculate on mechanisms which may operate to permit their coexistence in these waters. Within the six major parameters for interaction considered (Table 13), clear differences in response of the two species are evident between allopatric and sympatric populations.

When living separately, rainbow and cutthroat trout both apparently make rather broad use of lake habitats ranging from shallow littoral to open limnetic areas in near surface, midwater, and near bottom regions. In sympatry, rainbow appear to concentrate in the offshore, surface waters whereas cutthroat associate with littoral benthic areas. Our comments on habitat utilization by the two species in allopatry and sympatry need to be checked by studies specifically designed to examine temporal changes (diel, seasonal) as well as age differences. Nevertheless, the general pattern noted is similar to that described for allopatric and sympatric populations of several other salmonid pairs, such as cutthroat trout and Dolly Varden in coastal British Columbia lakes (Andrusak and Northcote 1970, 1971), Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Scandinavia (Nilsson 1955), normal and dwarf Arctic char in Sweden (Nilsson and Filipsson 1971), whitefish and char (Nilsson 1978), as well as

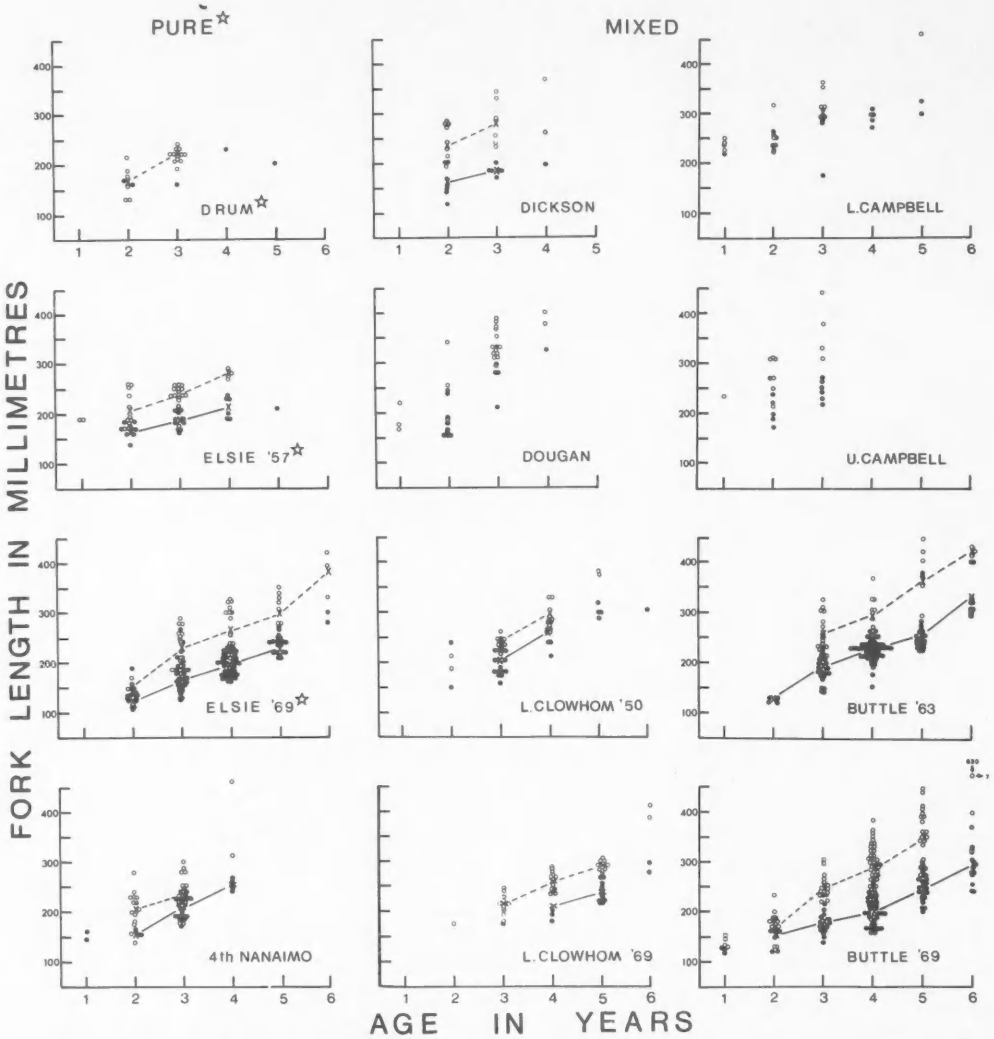

FIG. 5. Growth characteristics of sympatric populations of rainbow (●) and cutthroat (○) trout in the study lakes; averages indicated by ×, rainbow ——, cutthroat ----. Unless otherwise indicated, data from same years as in Fig. 2 with the following exceptions: Lower Campbell, 1951; Upper Campbell, 1951.

cisco and smelt in European lakes (Northcote and Rundberg1970; Nilsson 1979; Svärdson 1976). In sympatry, one of the pair tends to exploit the open water, limnetic habitat and the other the littoral or benthic habitat so that subadults and adults at least of each species are usually segregated spatially during much of the year.

Turning to relative abundance, rainbow trout in nearly all of the sympatric lakes seem to be much more abundant than the cutthroat, especially so when the probable bias of gillnet sampling for the latter species is considered. Again, this aspect of interaction has parellels in several of the European pairs referred to above where the form exploiting limnetic surface waters is usually numerically dominant over the littoral or benthic form.

Generalized feeding characteristics (Table 13) suggest that in allopatry, cutthroat utilize midwater prey and fish (stickleback, sculpins) in addition to surface and benthic prey whereas allopatric rainbow feed mainly on benthic prey with additional surface items, but rarely on fish. In sympatry, the two species tend to segregate in food habits, the rainbow

TABLE 10. Average length (mm) at age differences between sympatric rainbow and cutthroat trout populations (RB/CT).[a] Asterisks(*) indicate significant difference at $P < 0.05$.

Stock type	Population tested	Average length at age				
		2	3	4	5	6
"Pure"	Drum	167/216	b	b	b	b
	Elsie 1957	170/209	186/238*	211/279*	b	b
	Elsie 1969	128/154*	170/233*	200/268*	228/305*	285/381*
"Mixed"	Buttle 1963	b	192/256*	226/290	256/360*	333/425*
	Buttle 1969	162/170	186/256*	205/293*	252/352*	b
	Dickson	164/236*	185/283*	b	b	b
	Dougan	183/261	279/336*	b	b	b
	Fourth Nanaimo	157/206	210/233	253/385*	b	b
	Lower Campbell	b	266/335*	b	b	b
	Lower Clowhom	196/194	204/208*	242/276*	257/310*	291/400*
	Upper Campbell	215/277	243/366*	b	b	b

[a]Unless indicated, data from same years as in Fig. 3 with following exceptions: Lower Campbell, 1951; Upper Campbell, 1951.
[b]Data inadequate or lacking.

TABLE 11. Matrix for significant ($P < 0.05$) differences in length/age regressions between allopatric rainbow and cutthroat trout populations.[a]

Type	Cutthroat populations	"Pure" rainbow populations			
		Garibaldi	Healy	Lightning 1	Weaver
"Pure"	Cusheon			CT[b]	RB[b]
	Gosseneck	RB[b]			RB[b]
	Placid	RB[b]	RB[c]		RB[b]
	Twin	CT[c]	RB[c]		RB[c]
"Mixed"	Loon	CT[c]	RB[b]	CT[c]	CT[c]
	Mike	RB[b]	RB[c]	CT[b]	RB[b]
	Rainbow	RB[b]	RB[c]	RB[b]	RB[b]
	Ruby	CT[c]		CT[c]	CT[c]

[a]Data from same years as in Table 9.
[b]Species showing significantly higher intercept of length/age regression.
[c]Species showing significantly higher slope of length/age regression.

"taking over" the midwater food niche while cutthroat become even more piscivorous. Such a shift in cutthroat may be related to its larger mouth (Hartman 1956) and well developed dentition of the oral tract. There do not appear to be any particular morphological adaptations to planktivory in the rainbow trout (Hyatt 1980) as is evident in several European limnetic species via increased gill raker number (Svärdson 1979).

In allopatric populations rainbow trout attained larger body size and grew faster than the cutthroat whereas in sympatric populations just the reverse was observed, cutthroat in all cases being larger in size after 3 yr of age. Possibly the marked tendency of cutthroat to utilize larger prey items from the benthic community and to increase greatly piscivory (non-

TABLE 12. Lakes showing significant ($P < 0.05$) differences in length/age regressions between their sympatric rainbow and cutthroat trout populations.[a]

Stock type	Population tested	Significant length/age regression
"Pure"	Drum	Cutthroat[b]
	Elsie 1957	Cutthroat[b]
	Elsie 1969	Cutthroat[b]
"Mixed"	Buttle 1963	Cutthroat[c]
	Buttle 1969	Cutthroat[c]
	Dickson	Cutthroat[b]
	Dougan	Cutthroat[b]
	Fourth Nanaimo	Cutthroat[b]
	Lower Campbell	Cutthroat[c]
	Lower Clowhom	Cutthroat[c]
	Upper Campbell	Cutthroat[b]

[a]Data from same years as in Table 10.
[b]Species showing significantly higher intercept of length/age regression.
[c]Species showing significantly higher slope of length/age regression

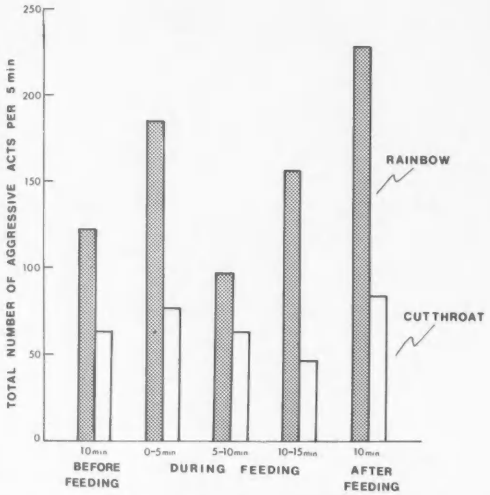

FIG. 6. Aggressive behavior of intraspecific paired rainbow and cutthroat trout associated with feeding in experimental tanks.

Salmo prey) would lead to such a growth enhancement compared with rainbow feeding on much smaller prey items (e.g. zooplankton) in limnetic regions. However, in two lakes (Mike and Rainbow) where cutthroat occur allopatrically with stickleback, the cutthroat never attain a large size or show rapid growth (Fig. 4). Although there may be many complicating factors (differences in lake productivity, angling pressure, and so on), it is interesting to note that in the one allopatric lake where cutthroat show best growth, they cohabit with other planktivorous species (kokanee, peamouth chub, and threespine stickleback) which may force them to exhibit the highest level of piscivory observed in an allopatric cutthroat population. The mechanism involved for the shift in growth advantage to the cutthroat in sympatry is not clear. D. M. Eggers (personal communication) suggests that higher energy expenditure in aggression of rainbow may reduce their growth in sympatry and if segregation of such populations are maintained interactively, as we speculate, this expenditure may be a continuing one. But why should the more aggressive species end up utilizing habitats with apparently poorer feeding opportunities, at least with respect to prey size? Also, there appear to be differences in feeding and growth of the two species between "pure" and "mixed" sympatric populations with dietary and possibly spatial segregation less well developed in pure sympatry (Fig. 1, Table 4). Compared with the latter, cutthroat in mixed sympatric lakes are larger and much more piscivorous (Fig. 3, Table 10). In these lakes, cutthroat which are too large to be dominanted by rainbow may become highly effective predators on small prey fishes (stickleback, sculpins) in nearshore habitat and thereby perhaps reinforce segregation of rainbow to offshore or midwater habitats.

The aquaria experiments on allopatric trout stocks strongly indicate that the rainbow are far more aggressive both intra- and inter-specifically than the cutthroat trout. The types of aggression were also different; rainbow, during the whole observation period associated with feeding, displayed "nipping," "chasing," and "lateral threats" while cutthroat never showed the latter but always "frontal threats," making it possible for them to expose their red hyoid slashes. Similar observations have been well described by Newman (1960). Nevertheless, confinement in small tanks may exaggerate behavioral responses of these trout (G. F. Hartman, personal communication) and observations on their aggressive interactions should be made under field conditions.

When taking food, the rainbow were much more vigorous, making spectacular dashes to capture food presented at the surface, whereas cutthroat approached the food items slowly and nibbled cautiously at them. Similar behavior patterns are well known to sport fishermen for these species. The rainbow often leap out of the water when taking food at the surface whereas the cutthroat snap cautiously at such prey from beneath, more like the species of *Salvelinus*.

Clearly the single most evident and yet puzzling result of this study has been the finding that in allopatry rainbow trout tend to grow faster and attain larger size than cutthroat whereas in sympatry the reverse is true. Factors influencing these controversial characteristics might be (1) morphology, especially of the oral tract; (2) behavior, especially aggressiveness and feeding; and (3) spawning and survival of young.

Although the mouth size of cutthroat is known to be larger relative to that of rainbow, there may be important differences in this morphological characteristic within stocks of the same species, e.g. between allopatric and sympatric populations. Selective pressures in sympatry should favor larger mouth size than in allopatry and hence the ability to feed earlier on larger prey items, perhaps thereby gaining a growth advantage (cf. *Cottus rhotheus* vs. *C. asper*, Northcote 1954).

It has been well documented under laboratory conditions, at least, that rainbow are much more aggressive than cutthroat. This in allopatry may favor the more aggressive individuals and hence promote more rapid growth, as has been observed (Fig. 4, Table 9). Cutthroat, on the other hand, are less aggressive, similar to *Salvelinus* species (Newman 1960). Thus, aggressiveness is of less significance to cutthroat in

TABLE 13. Summary of interactions between allopatric and sympatric adult populations of rainbow and cutthroat trout in coastal British Columbia lakes.

Interaction parameter	Allopatry		Sympatry	
	Rainbow	Cutthroat	Rainbow	Cutthroat
Spatial distribution	Broad (littoral–limnetic)	Broad (littoral–limnetic)	Upper limnetic	Benthic–littoral
Relative abundance	Variable	Variable	Dominant	Subordinate
Feeding	Benthic with some midwater and surface; rarely piscivorous	Midwater with some benthic and surface; often piscivorous	Mainly benthic and midwater, some surface; rarely piscivorous	Mainly piscivorous, some benthic and surface
Body size	Larger	Smaller	Smaller	Larger
Growth rate	Faster	Slower	Slower	Faster
Aggression	High	Low	High	Low

allopatry. When living in sympatry with rainbow, fast growth rate would be of high survival value for the less aggressive cutthroat.

Also of importance to this problem, of course, may be differences in timing and location of spawning as well as the consequent survival of offspring. We have not examined these aspects but they should be investigated in allopatric and sympatric populations of the trout.

In coastal lakes of British Columbia, close as they are to large urban centers, there is a heavy demand for waters to readily provide reasonable catches to a large number of anglers. At the same time there is also a demand by a smaller but sophisticated angling component for the opportunity to catch a few large fish requiring considerable skill. This dual demand could possibly best be met by lakes with sympatric rainbow and cutthroat populations. The former species would provide relatively easy catches of smaller sized trout whereas the latter would provide an opportunity to catch a few large-sized individuals demanding considerable skill.

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ANDRUSAK H., AND T. G. NORTHCOTE. 1970. Management implications of spatial distribution and feeding ecology of cutthroat trout and Dolly Varden in coastal British Columbia lakes. B. C. Fish Wildl. Branch Fish. Manage. Publ. 13. 14 p.

1971. Segregation between adult cutthroat trout (*Salmo clarki*) and Dolly Varden (*Salvelinus malma*) in small coastal British Columbia lakes. J. Fish. Res. Board Can. 28: 1259–1268.

BRIAN, M. V. 1956. Segregation of species of the ant genus *Myrmica*. J. Anim. Ecol. 25: 319–337.

CROSSMAN, E. J. 1959. A predator–prey interaction in freshwater fish. J. Fish. Res. Board Can. 16: 269–281.

EFFORD, I. E., AND K. TSUMURA. 1973. A comparison of the food of salamanders and fish in Marion Lake, British Columbia. Trans. Am. Fish. Soc. 102: 33–47.

EVEREST, F. H., AND D. W. CHAPMAN. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board Can. 29: 91–100.

FABRICIUS, E. 1953. Aquarium observations on the spawning behavior of the char, *Salmo alpinus*. Rep. Inst. Freshwater Res. Drottningholm 34: 14–48.

GLOVA, G. J. 1978. Pattern and mechanism of resource partitioning between stream populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki clarki*). Ph.D. thesis, Dep. Zool., Univ. British Columbia, Vancouver. 185 p.

GRIMÅS, U. 1961. The bottom fauna of natural and impounded lakes in northern Sweden (Ankarvattnet and Blåsjön). Rep. Inst. Freshwater Res. Drottningholm 42: 183–237.

HARTMAN, G. F. 1956. A taxonomic study of cutthroat trout, *Salmo clarki clarki* Richardson, rainbow trout *Salmo gairdneri* Richardson and reciprocal hybrids. M. A. thesis, Dep. Zool., Univ. British Columbia, Vancouver. 71 p.

1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 22: 1035–1081.

HARTMAN, G. F., AND C. A. GILL. 1968. Distributions of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. J. Fish. Res. Board Can. 25: 33–48.

HUME, J. M. B. 1978. Planktivorous feeding and habitat utilization of sympatric and experimentally segregated populations of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden char (*Salvelinus malma*). M.Sc. thesis, Dep. Zool., Univ. British Columbia, Vancouver. 143 p.

HYATT, K. D. 1980. Mechanisms of food resource partitioning and the foraging strategies of rainbow trout (*Salmo gairdneri*) and kokanee (*Oncorhynchus nerka*) in Marion Lake, British Columbia. Ph.D. thesis, Dep. Zool., Univ. British Columbia,

Vancouver. 258 p.

JOHANNES, R. E., AND P. A. LARKIN. 1961. Competition for food between redside shiners (*Richardsonius balteatus*) and rainbow trout (*Salmo gairdneri*) in two British Columbia lakes. J. Fish. Res. Board Can. 18: 203–220.

KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Rep. Inst. Freshwater Res. Drottningholm 39: 55–98.

MACPHEE, C. 1961. An experimental study of competition for food in fish. Ecology 44: 666–681.

MAGNUSON, J. J. 1962. An analysis of aggressive behavior, growth, and competition for food and space in medaka (*Oryzias latipes* (Pisces, Cyprinodontidae)). Can. J. Zool. 40: 313–363.

MCMYNN, R. G., AND P. A. LARKIN. 1953. The effects on fisheries of present and future water utilization in the Campbell River drainage area. B. C. Game Comm. Manage. Publ. 2. 61 p.

NEWMAN, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. 29: 64–81.

1960. A comparative study of the residential behavior of juvenile salmonids. Ph.D. thesis, Dep. Zool., Univ. British Columbia, Vancouver. 295 p.

NILSSON, N.-A. 1955. Studies on the feeding habits of trout and char in north Swedish lakes. Rep. Inst. Freshwater Res. Drottningholm 36: 163–225.

1963. Interaction between trout and char in Scandinavia. Trans. Am. Fish. Soc. 92: 276–285.

1964. Effects of impoundment on the feeding habits of brown trout and char in Lake Ransaren (Swedish Lappland). Verh. Int. Verein. Limnol. 15: 444–452.

1967. Interactive segregation between fish species, p. 295–313 *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

1978. The role of size-biased predation in competition and interactive segregation in fish, p. 303–325. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

1979. Food and habitat of the fish community of the offshore region of Lake Vänern, Sweden. Rep. Inst. Freshwater Res. Drottningholm 58: 126–139.

NILSSON, N.-A. AND O. FILIPSSON. 1971. Characteristics of two discrete populations of Arctic char (*Salvelinus alpinus* L.) in a north Swedish lake. Rep. Inst. Freshwater Res. Drottningholm 51: 90–108.

NORTHCOTE, T. G. 1954. Observations on the comparative ecology of two species of fish, *Cottus asper* and *Cottus rhotheus* in British Columbia. Copeia 1954: 25–28.

1973. Some impacts of man on Kootenay Lake and its salmonoids. Great Lakes Fish. Comm. Tech. Rep. 25. 46 p.

NORTHCOTE, T. G., AND R. CLAROTTO. 1975. Limnetic macrozooplankton and fish predation in some coastal British Columbia lakes. Verh. Int. Verein. Limnol. 19: 2378–2393.

NORTHCOTE, T. G., AND P. A. LARKIN. 1956. Indices of productivity in British Columbia lakes. J. Fish. Res. Board Can. 13: 515–540.

1963. Western Canada, chap. 16, p. 451–485. *In* D. G. Frey [ed.] Limnology of North America. University of Wisconsin Press, Madison, WI.

NORTHCOTE, T. G., AND H. RUNDBERG. 1970. Spatial distribution of pelagic fishes in Lambarfjärden (Mälaren, Sweden) with particular reference to interaction between *Coregonus albula* and *Osmerus eperlanus*. Rep. Inst. Freshwater Res. Drottningholm 50: 133–167.

NORTHCOTE, T. G., C. J. WALTERS, AND J. M. B. HUME. 1978. Initial impacts of experimental fish introductions on the macrozooplankton of small oligotrophic lakes. Verh. Int. Verein. Limnol. 20: 2003–2012.

NYMAN, L. 1972. A new approach to the taxonomy of the "*Salvelinus alpinus* species complex." Rep. Inst. Freshwater Res. Drottningholm 52: 103–131.

SCHUTZ, D. C., AND T. G. NORTHCOTE. 1972. An experimental study of feeding behavior and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). J. Fish. Res. Board Can. 29: 555–565.

SHEPHERD, B. G. 1973. Temporal and spatial differences in movement of cutthroat trout in Placid Lake, British Columbia. M.Sc. thesis, Dep. Zool., Univ. British Columbia, Vancouver. 92 p.

SINCLAIR, D. C. 1965. The effects of water level changes on the limnology of two British Columbia coastal lakes, with particular reference to the bottom fauna. M.Sc. thesis, Dep. Zool., Univ. British Columbia, Vancouver. 84 p.

SVÄRDSON, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshwater Res. Drottningholm 55: 144–171.

1979. Speciation of Scandinavian *Coregonus*. Rep. Inst. Freshwater Res. Drottningholm 57: 3–95.

Short-term Forecasting in Marine Fish Stocks

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STOCKER, M., AND R. HILBORN. 1981. Short-term forecasting in marine fish stocks. Can. J. Fish. Aquat. Sci. 38: 1247–1254.

The predictive power of stock production models and simple time series methods was considered for five marine fish stocks. The distinction between model fitting and forecasting future short-term catch is discussed, as is the difference between techniques to forecast short-term yield, and techniques to calculate long-term management practice. Fox's procedure for fitting Pella and Tomlinson's stock production model, Schnute's method for fitting Schaefer's model, and Gulland's method are all considered. We found that all methods except that of Gulland work well for some stocks, and the relative performance of the methods depends upon the exploitation history of the stock. In several instances one of the best forecasts of next year's catch per unit effort (CPUE) was the previous year's CPUE, emphasizing the fact that a good forecasting technique may have no utility in determining management policies.

Key words: production models, catch and effort, fisheries, management, catch forecasting, time series

STOCKER, M., AND R. HILBORN. 1981. Short-term forecasting in marine fish stocks. Can. J. Fish. Aquat. Sci. 38: 1247–1254.

Nous examinons la capacité prévisionnelle de modèles de production de stocks et de simples méthodes de séries chronologiques pour cinq stocks de poissons de mer. Nous considérons la distinction entre l'adéquation des modèles et la prévision à court terme de prises futures, de même que la différence entre techniques de prévision de rendement à court terme et techniques permettant d'arrêter une gestion à long terme. Nous examinons la méthode de Fox d'adéquation du modèle de production de stocks de Pella et Tomlinson, la méthode de Schnute d'adéquation du modèle de Schaefer et, enfin, la méthode de Gulland. Nous constatons que toutes ces méthodes, sauf celle de Gulland, sont satisfaisantes pour certains stocks, et que la performance relative des méthodes dépend de l'exploitation passée du stock. Dans plusieurs cas, une meilleure prévision des prises par unité d'effort (PPUE) de la prochaine année a été les PPUE de l'année précédente. Ceci fait ressortir l'inutilité, dans certains cas, d'une bonne technique de prévision dans l'élaboration de politiques de gestion.

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THE major charge of fisheries managers is to determine long-term policies that will provide near-optimum returns from the stocks. In contrast, users of the resource frequently want short-term forecasts to determine decisions regarding investment, expenditure, and fishing location. These two goals, long-term management and short-term forecastings, may require very different methods.

For example, long-term management of Pacific salmon is generally based on a fixed escapement policy. The desired escapement is often determined from some form of stock production model, generally, either that of Ricker (1954, 1958), or less formal methods. From past stock production data, the optimum escapement is estimated and the future long-term expected yields are calculated. On the other hand, the expected run for a given year is forecasted on a different basis. Factors such as freshwater runoff while the brood was in freshwater, average temperatures, and size of parental spawning stock are frequently used.

In marine fisheries, stock production models (e.g. Schaefer 1954, 1957; Gulland 1961) are frequently used to predict long-term effects of regulations. Short-term forecasting, on the other hand, has received less emphasis. This is probably because marine fisheries are generally regulated by quotas, and fishermen perceive the catch more than the catch per unit effort (CPUE) as a measure of fishing quality.

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If one assumes that effort will change little from year to year, then increases or decreases in the quota will directly result in increases or decreases in catch for individual fishermen.

The above remarks are predicated on the assumption that fishermen are not moving between fisheries in an effort to find the best returns per unit effort expended. If fishermen do seek out such opportunities (for instance Hilborn and Ledbetter 1979), or cease to fish when CPUE becomes poor, then short-term forecasting becomes an important aspect of management.

While we acknowledge that catch per unit effort may be of primary interest, catch per unit effort generally depends upon the effort; higher efforts mean lower catch per unit effort. Thus, in our analysis we actually forecast catch given next year's effort (we assume we know it perfectly). In practice a biologist should provide a forecast for several levels of effort. This would recognize that the two are interdependent and one cannot forecast effort perfectly.

In this paper we explore methods for forecasting short-term (annual) changes in CPUE. We begin with a discussion of methods for making catch forecasts, consider our expectations in light of the exploitation history of stocks, and examine seven methods for forecasting catch for five marine fish stocks.

Methods of Forecasting

Among the large number of methods used for long-term management of marine stocks, the most commonly used methods are based upon some stock production relationship. Examples are those of Gulland (1961), Schaefer (1954, 1957), and Pella and Thomlinson (1969). These three stock production models have similar biological assumptions. They assume that (1) an unfished stock will grow to some maximum and stay at that level, (2) as population increases the per capita rate of increase decreases to zero at the unfished equilibrium density, and (3) catch per unit effort reflects stock abundance.

Although each of these methods assumes that catch per unit effort is the index of stock abundance, if other measures of abundance are available, such as echo soundings or experimental surveys, these data can generally be substituted directly into the stock production models as a surrogate for catch per unit effort. The catchability coefficient then assumes a slightly different meaning.

To make catch forecasts for next year ($t + 1$), we use seven methods. Four methods employ stock production models, and three methods rely on some form of time series analysis.

Gulland's equilibrium approximation method relates stock abundance (CPUE) to average effort levels

$$(1) \quad U_t = a + b\,\bar{E}_t$$

where: U_t = catch per unit effort in year t, $\bar{E}_t$ = averaged effort over K preceding years for year t (K is the average number of years a year-class contributes to the fishery), and a and b are regression coefficients. Given a time series of U_t's and E_t's a linear regression yields estimates of a and b. These are used in the corresponding relationship between catch and effort

$$(2) \quad \hat{C}_{t+1} = a\,\bar{E}_{t+1} + b\,\bar{E}^2_{t+1}$$

to forecast next year's catch ($\hat{C}_{t+1}$) based on next year's averaged effort ($\bar{E}_{t+1}$).

Schaefer's model is commonly used for catch–effort analysis. We use a difference equation version (Walters and Hilborn 1976; Uhler 1980; Hilborn 1979) in its linear regression form to estimate the model parameters

$$(3) \quad \left(\frac{U_{t+1}}{U_t}\right) - 1 = r - \frac{r}{qk}\,U_t - q\,E_t$$

where: U_{t+1} = catch per unit effort in year $t + 1$, U_t = catch per unit effort in year t, E_t = fishing effort in year t, r = growth parameter, k = unfished equilibrium stock size, and q = proportion of fish stock caught per unit fishing effort.

Given several years of observed values of U_t's and E_t's, estimates of r, k, and q are obtained from (3) by multiple regression. From estimates of these parameters next year's population ($\hat{N}_{t+1}$) and catch ($\hat{C}_{t+1}$) are forecast from:

$$(4) \quad \hat{N}_{t+1} = N_t + N_t r\left(1 - \frac{N_t}{k}\right) - C_t$$

and

$$(5) \quad \hat{C}_{t+1} = \hat{N}_{t+1}\,E_{t+1}\,q$$

where N_t = population in year t, and C_t = catch in year t.

The generalized stock production model (Pella and Tomlinson 1969) has been developed into a commonly used computer package by Fox (1975). We employ his formulation at equilibrium with averaged fishing effort as one of the forecast methods:

$$(6) \quad U_t = \left(\frac{Kq^{m-1}}{H} + \frac{q^m}{H}\bar{E}_t\right)^{\frac{1}{m-1}}$$

where: U_t = catch per unit effort in year t, $\bar{E}_t$ = averaged fishing effort during year t, q = catchability coefficient, and K, H, and m are constant parameters of the generalized stock production model. Given a data set of U_t's and $\bar{E}_t$'s, a least squares criterion is used to obtain best estimates of q, K, H, and m (Fox 1975). Catch forecasts for next year ($t + 1$) are made by using the relationship:

$$(7) \quad \hat{C}_{t+1} = \bar{E}_{t+1}\left(\frac{Kq^{m-1}}{H} + \frac{q^m}{H}\bar{E}_{t+1}\right)^{\frac{1}{m-1}}$$

where: $\bar{E}_{t+1}$ = averaged observed fishing effort in year $t + 1$.

The fourth method employing surplus production models is Schnute's (1977) approximation of the continuous Schaefer model. Again given a time series of U_t's and E_t's, estimates of the three model parameters r, k, and q are obtained by regressing one variable on two:

$$(8) \quad \ln\left(\frac{U_{t+1}}{U_t}\right) = r - q\left(\frac{E_t + E_{t+1}}{2}\right) - \frac{r}{qk}\left(\frac{U_t + U_{t+1}}{2}\right).$$

Symbols are as described above for the linear version.

Schnute's equation (31) for $\tau = 1$ is used to forecast next year's catch ($\hat{C}_{t+1}$) for the observed effort levels (E_{t+1}):

$$(9)\quad \hat{C}_{t+1} = \frac{qk}{r} E_{t+1} \ln\left[1 + \left(\frac{r - qE_t}{r - qE_{t+1}}\right)\left(\frac{\exp(r - qE_{t+1}) - 1}{1 - \exp - (r - qE_t)}\right)\left(1 - \exp\left(-\frac{r}{qk}\frac{C_t}{E_t}\right)\right)\right].$$

If we stand back from the fisheries perspective, we recognize that we have a series of two variables from which we wish to forecast the next value of one of them. This is a standard problem in time series analysis (Box and Jenkins 1970) for which there are well-developed techniques. Forecasting in time series analysis involves using past observations to forecast future ones. The stock production models discussed above use a structure (the model) based upon biological assumptions to forecast new observations. A more commonly used form of time series analysis is to use autoregressive models, where future observations are computed as linear functions of past observations. The simplest method is to assume that next year's catch per unit effort will be the same as this year's. That is:

$$(10)\quad \hat{U}_{t+1} = U_t$$

thus

$$(11)\quad \hat{C}_{t+1} = U_t E_{t+1}.$$

If we observe that U's change very slowly (high serial correlations between them), then U_t may forecast U_{t+1} well. If, however, we believe that there is no serial correlation, but that catches are simply a random variable with a mean and variance, then we might believe that the running average catch ($\bar{C}$) would be the best predictor of the next catch.

$$(12)\quad \hat{C}_{t+1} = \frac{C_1 + C_2 + C_3 \ldots C_t}{t}.$$

Alternatively, we can view our fisheries system as a black box with a single output (catch) and a single input (effort). A conventional time series approach to this type of problem is to generate a linear model such as:

$$(13)\quad C_{t+1} = p_1C_1 + p_2C_2, \ldots, p_tC_t + p_{t+1}E_1 + p_{t+2}E_2, \ldots, p_{2t+1}E_{t+1}.$$

In general, autoregressive models usch as (13) can be written as multiple regressions, except in (13) we have as many parameters as data points. In the fisheries context it seems clear that next year's catch should depend upon next year's effort, and past catches. It is not so clear that it should depend upon past efforts. To test these time series methods we used an autoregressive approach similar to (13) described by Young (1974). We considered C_{t+1} to depend upon E_{t+1}, C_t, C_{t-1}, and C_{t-2}.

We make no claim of using the best time series methods, but rather wish primarily to point out their existence as an alternative to stock production models, and to try out a simple one. Further it is clear that two values for 15–25 years constitute a very small data set by the standards of most time series analyses, and good forecasts of catches would probably utilize many biophysical factors in addition to catch and effort.

Recently, Saila et al. (1980) and Mendelssohn (1981) have used time series methods to forecast stock abundance. Both papers obtained good forecasts of seasonal catches using Box–Jenkins (1970) methods. In both papers long time series were available (monthly catches for several years) and there were very consistent seasonal trends in the data. The time series examined in this paper are considerably shorter, and less regular.

The Concept of Forecast

At any point in time our knowledge of the stock is contained in the effort history $E_1, \ldots, E_n$, and the catch per unit effort history $U_1, \ldots, U_n$. Given an effort level for next year and our stock history, our goal is to forecast C_{t+1}.

If we have a time series of data for a fish stock (E_t's, U_t's) for n yr, we can see which type of model best fits our data using normal least squares procedures. Discussions in Schaefer (1957), Schnute (1977), and Fox (1975) consider how this is done. Emerging is a statistic that tells us how much of the variation we were able to explain — Schnute calls this the failure index. A perfect fit of model to data would explain

TABLE. 1. Comparison of catch forecasts of seven methods for northern Hecate Strait rock sole.

Year of forecast $t+1$	Data series $t = 1,2,\ldots,n$	n	Observed catch in year $t+1$ (t)	Observed effort in year $t+1$ (h)	Forecast catch in year $t+1$ (t)						
					Method						
					Gulland	Linear	Fox	Schnute	U_t	$\bar{C}$	Time series
1969	1954–68	15	1230	1577	362	844	967	367	710	735	1831
1970	1954–69	16	455	1034	873	874	985	1121	807	766	1173
1971	1954–70	17	895	2295	226	1463	1177	875	1010	748	1790
1972	1954–71	18	230	821	800	359	834	284	320	756	830
1973	1954–72	19	180	391	482	175	476	116	109	729	159
1974	1954–73	20	220	688	714	436	718	370	317	701	515
1975	1954–74	21	562	878	781	428	857	280	281	678	459
1976	1954–75	22	892	1622	652	1262	1101	982	1038	673	871
1977	1954–76	23	427	1186	792	716	956	601	652	682	657
1978	1954–77	24	394	895	743	425	877	323	322	672	412

TABLE 2. Summary of total variance (σ^2), unexplained variation (D), and ($1 - D/\sigma^2$) for seven forecast methods for five marine stocks.

		Forecast					
		Gulland		Linear		Fox	
Stock	σ^2	D	$(1 - D/\sigma^2)$	D	$(1 - D/\sigma^2)$	D	$(1 - D/\sigma^2)$
Northern Hecate Strait rock sole	109.5×10^3	239.6×10^3	−1.19	95.0×10^3	0.13	177.4×10^3	−0.62
Ranking of method		VII		II		V	
Middle Hecate Strait rock sole	76.1×10^3	158.9×10^3	−1.09	40.2×10^3	0.47	31.0×10^3	0.59
Ranking of method		VI		IV		I	
Hecate Strait English sole	53.3×10^3	73.7×10^3	−0.38	11.9×10^3	0.78	34.1×10^3	0.36
Ranking of method		VII		I		II	
Eastern Pacific yellowfin tuna	955.8×10^6	260.6×10^7	−1.73	257.2×10^6	0.73	135.3×10^7	−0.42
Ranking of method		V		I		IV	
California sardines	145.8×10^8	539.8×10^8	−2.70	140.4×10^8	0.04	751.0×10^8	−4.15
Ranking of method		IV		III		V	
Average ratio $\frac{1}{5}\sum_{i=1}^{i=5}(1 - D_i/\sigma_i^2)$			−1.42		0.43		−0.85

100% of the variation; a poor fit would explain none. This statistic is analogous to r^2 of regression.

We cannot conclude that the model that fits the data best is the preferred model in the sense that "preferred" refers to the success of forecasting future catches. As a trivial example, consider the following model:

$$U_{t+1} = p_1 + p_2V_t + p_3U_t^2 \ldots p_{20}U_t^{20} \quad (14)$$

where

$p_1 \ldots p_{20}$ are parameters estimated by ordinary least squares. If we had a time series of 25 U's the above model would undoubtedly explain a high portion of the variation in the U's, but the model would probably be totally worthless for forecasting future catches.

Fitting is easier than forecasting. To test the forecasting power of a model, we use the following method. We have a time series of E_t's and U_t's for 20–30 years. We forecast C_{16} based upon the E_t's and U_t's up to and including year 15, and using E_{16}. We then advance 1 year, use the data up to and including year 16, and forecast C's for year 17. We repeat this procedure through our entire time series. Formally:

$$\hat{C}_{t+1} = f(E_1, \ldots, E_{t+1}; U_1, \ldots, U_t)$$

$$D = \frac{1}{(N+1) - 16}\sum_{t=16}^{t=N}(C_t - \hat{C}_t)^2 \quad (15)$$

where D = unexplained variation, N = final year of prediction. We compute the D statistic for each prediction method. The smaller the D value, the better the method at forecasting.

Results

Table 1 shows the results of catch forecasts for the trawl

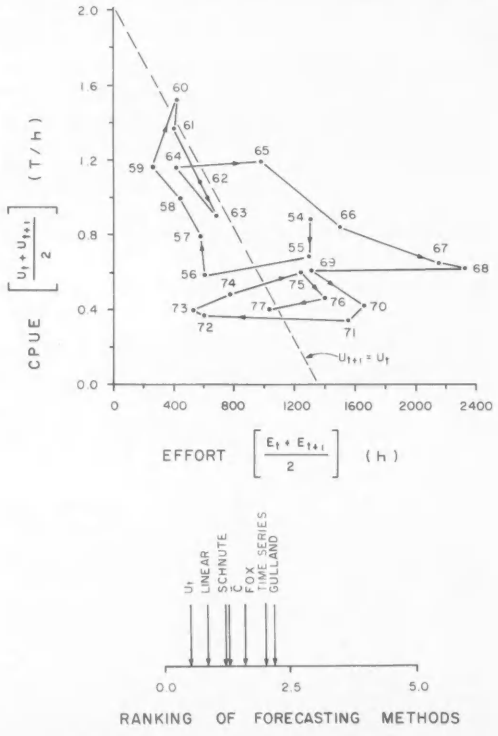

FIG. 1. Exploitation history of the northern Hecate Strait rock sole stock (1954–77), and ranking of forecasting methods. (Data from Westrheim 1980.)

method							
Schnute		U_t		$\overline{C}$		Time series	
D	$(1 - D/\sigma^2)$	D	$(1 - D/\sigma^2)$	D	$(1 - D/\sigma^2)$	D	$(1 - D/\sigma^2)$
134.1×10^3 III	−0.22	58.6×10^3 I	0.46	137.7×10^3 IV	−0.26	219.4×10^3 VI	−1.00
34.3×10^3 II	0.55	39.7×10^3 III	0.48	81.9×10^3 V	−0.08	883.0×10^3 VII	−10.60
45.2×10^3 III	0.15	53.4×10^3 V	−0.01	57.5×10^3 VI	−0.08	52.9×10^3 IV	0.01
491.7×10^6 II	0.49	681.7×10^6 III	0.29	375.6×10^7 VI	−2.93	800.0×10^7 VII	−7.37
901.7×10^7 II	0.38	792.6×10^7 I	0.46	964.2×10^8 VI	−5.61	206.0×10^9 VII	−13.13
	0.26		0.34		−1.79		−6.42

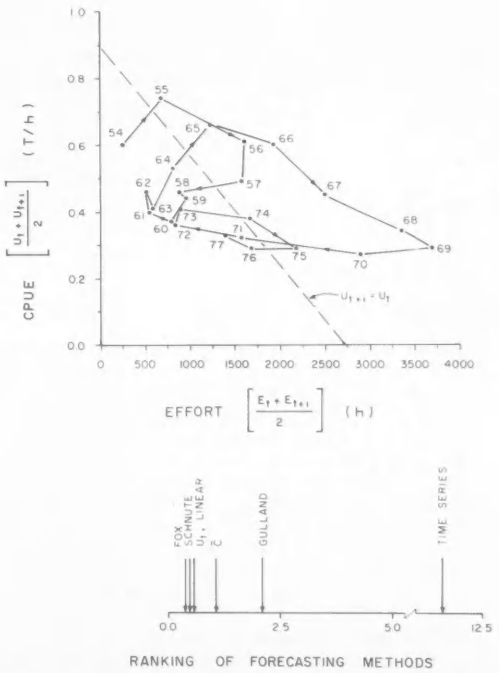

FIG. 2. Exploitation history of the middle Hecate Strait rock sole stock (1954–77), and ranking of forecasting methods. (Data from Westrheim 1980.)

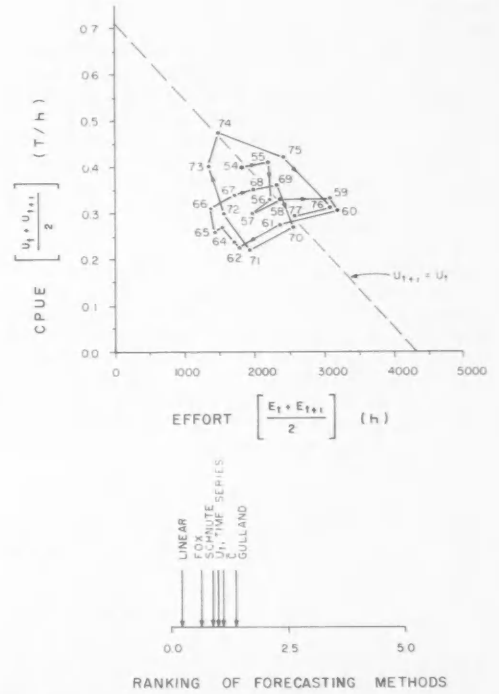

FIG. 3. Exploitation history of the Hecate Strait English sole stock (1954–77), and ranking of forecasting methods. (Data from Westrheim 1980.)

fishery on rock sole in northern Hecate Strait, British Columbia (Westrheim 1980). The data series begins in 1954; the first 15 years are used to forecast the 16th year 1969. The first row on Table 2 gives the unexplained variation (D) for each of the seven methods, and total variance (σ^2) between the observed catch, and the average catch over the years we were forecasting. Also shown is $(1 - D/\sigma^2)$ which is analogous to r^2 of regression.

Figure 1 shows the catch–effort history of the northern Hecate Strait rock sole fishery. The data are plotted in the form used by Schnute's method, that is the abscissa is $E_t + E_{t+1}/2$ and the ordinate is $U_t + U_{t+1}/2$. The broken line is the $U_{t+1} = U_t$ isocline generated by Schnute's method for the entire series. U should decline to the right of the isocline and should increase to the left of it. The northern Hecate Strait rock sole has had periods of increase and decline. It has not hovered closely about an equilibrium and there are serial correlations in the U's, that is, U's of adjacent years are correlated. The bottom of Fig. 1 shows the rankings of the various forecast methods. It is not surprising that U_t forecasts U_{t+1} well. It is discouraging that the stock production model based forecasts do no better — this tells that there is obviously more going on than can be explained by stock production models.

Figure 2 shows the exploitation history of the middle Hecate Strait rock sole stock (Westrheim 1980), and the relative performance of the various forecast methods. As in the northern stock there have been periods of decline and increase, but the models (except that of Gulland) do fit the data better here. All of the stock production based models and the method using U_t explain 50% of the total variance in catches. The differences between these methods are slight.

Figure 3 shows the exploitation history of Hecate Strait English sole (Westrheim 1980). The data are closely grouped and long runs of serial correlations are noticeably lacking. Thus, it is not surprising that the forecasting method using U_t is poor relative to the others, among which the linear method performs best.

Figure 4 shows the exploitation history of eastern Pacific yellowfin tuna (*Thunnus albacares*) during 1953–76 (Pella and Tomlinson 1969; IATTC 1978). The history is interesting because the first 12 years of data are closely grouped about the equilibrium isocline. From 1969 to 1976 the effort was increased nearly threefold with only small associated declines in CPUE. Despite the strong serial correlation in efforts, such correlations do not exist in CPUE, and thus the method using U_t is not particularly good. Again the linear model produces the best forecasts.

An anonymous reviewer pointed out that the dynamics of this tuna fishery changed in 1969 and suggested we should fit the 1953–68 data separately from the 1969–76 data. This is fine for fitting of models, but will not work for forecasting simply because when we are trying to forecast the 1969 catch, we have only the 1953–68 data available. We do not know if the system has changed until we have seen several years' data. If other information about the fishing pattern suggests that things have changed fundamentally, we could discount pre-1969 data. This emphasizes the futility of cookbook approaches; in any one year one must ask if you believe that all the past data are applicable to today's problem. We are

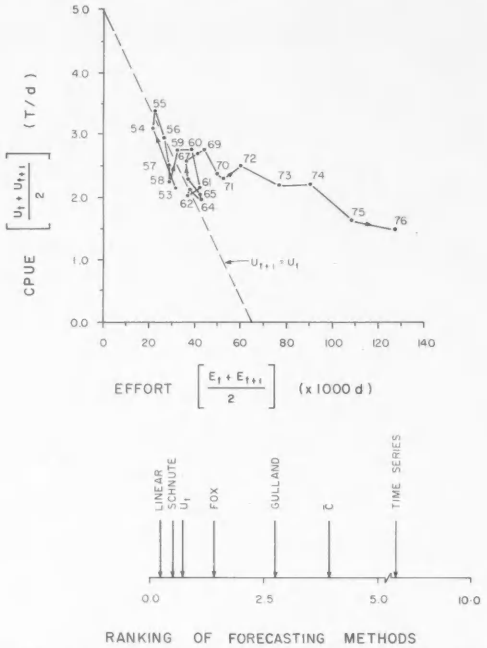

FIG. 4. Exploitation history of eastern Pacific yellowfin tuna (1953–76), and ranking of forecasting methods. (Data from Pella and Tomlinson 1969, and IATTC 1978.)

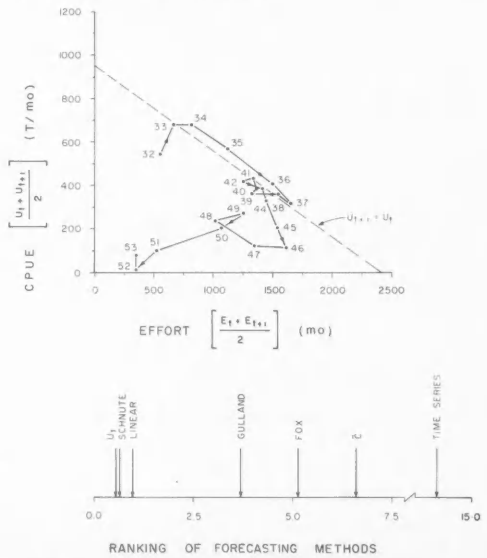

FIG. 5. Exploitation history of California sardine (1932–53), and ranking of forecasting methods. (Data from Marr 1963.)

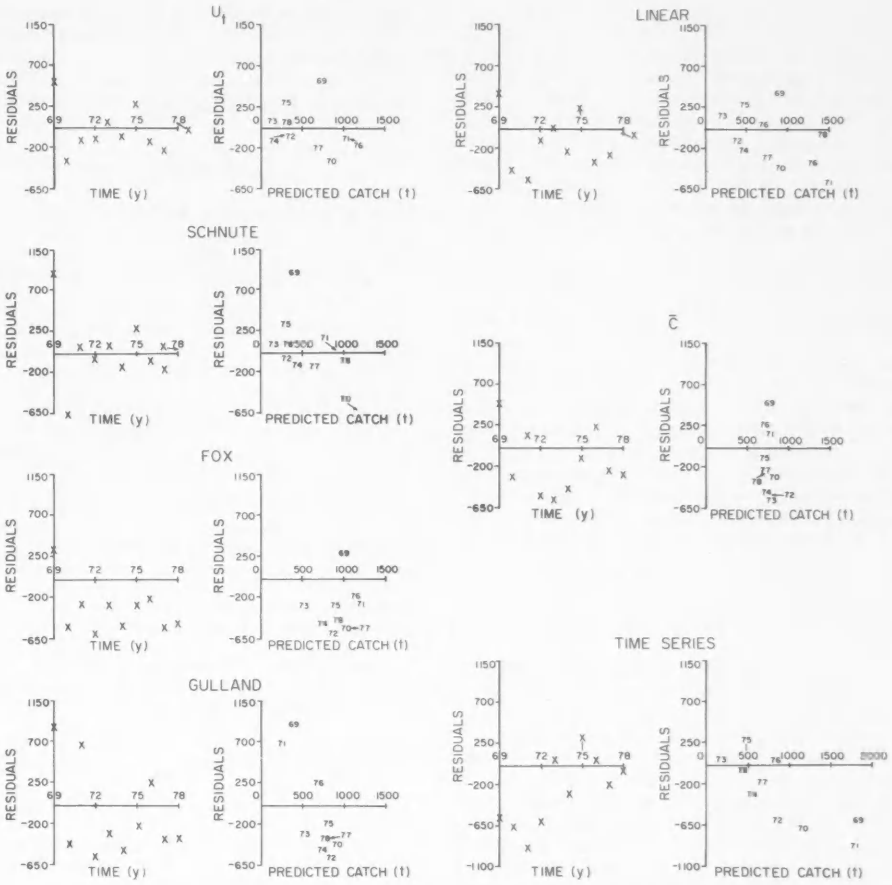

FIG. 6. Residual plots of catch forecasts of seven methods for northern Hecate Strait rock sole.

attempting to illustrate a range of approaches to forecasting, not to generate a cookbook. If one has particular information about a stock, it should certainly be used.

Figure 5 demonstrates a different stock history — that of the Pacific (California) sardine (*Sardinops sagax*) which, at least according to Marr (1963), was driven commercially extinct. It is obvious that there are strong serial correlations in the U's, and thus not surprising that U_t is a good forecast method. Since the stock declined on the left-hand side of the isocline (where it should increase), it is also clear that stock production models totally fail to capture the dynamics of this fishery. Thus, it is even more surprising that Schnute's method and the linear model do as well as they do.

Table 2 shows that the best forecasting method differes greatly from stock to stock. The linear method, Fox's method, and using U_t all prove to be best for individual stocks. The bottom row of Table 2 gives the average of $(1 - D/\sigma^2)$ for each method; the linear method, U_t, and Schnute's method are all good performers. Fox's method is half as good as the previous three, and Gulland's method and using the running average catch (12), and time series analysis are least successful.

Often the analysis of residuals provides information about the performance of a model. Figure 6 shows the residuals from the forecast for north Hecate Strait rock sole. If the residuals were homogeneous and contained no serial correlations, then they would contain no information that could be used to improve forecasts. Figure 6 shows that this is rarely the case. The linear, Gulland, Fox, and $\bar{C}$ methods all show negatively biased residuals. Autocorrelations are not so pronounced. We thus suspect that most of the methods could be improved by adding an additional term to adjust the forecasts by past average residuals. However, this is exactly what many time series methods do, and we recommend that readers look at Box and Jenkins (1970), Saila et al. (1980), and Mendelssohn (1981).

Discussion

It would be tempting to suggest that the linear form of the Schaefer model or Schnute's method should be used to formulate management regulations, as they produced the best forecasts. Nothing could be more deceptive. The use of U_t to forecast U_{t+1} worked very well, yet clearly has no information usable for formulating long-term management regulations. We cannot even conclude that Gulland's method, which produced poor forecasts, is necessarily a poor long-term management tool. Our results reflect only upon short-term forecasts.

We now have some good prospective methods for such short-term forecasting. A management biologist must choose the best method for his short-term forecast, and we have provided not only a methodology for selection, but we suggest that one can discard at least Gulland's method a priori. We cannot make any specific recommendation regarding the relative merits of Fox's, Schnute's, or the linear method; they should probably all be tried for any specific stock. It appears that formal time series methods also deserve considerable attention, particularly in light of the residuals analysis.

The proportion of total variance in catch explained by a forecast method (Table 2) is a statistic of the method's performance. The variance is a statistic available only with hindsight; the average catch is computed from the entire set of years after the 15th one. If we wish to examine how well a method forecasts, given only the data available at the time of forecasting, the variance should use the sum of squares generated using the running average catch (the sixth method of Table 2).

For the Hecate Strait stocks of rock sole and English sole, the new ratio would be similar since the ration (D/σ^2) for the method is near 1.0. For the tuna and sardine stocks the differences are dramatic. For tuna, the linear method explains all but 7% of the variability generated using running average catch; for sardines the method using U_t explains all but 8%, and Schnute's method explains all but 9%. Although these relatively good forecasts do not imply a fundamental understanding of the system, they are nevertheless impressive.

Finally, we return to the influence of the stock's exploitation history on the amount of the variability we can explain. If we believe that the changes in U are due to changes in effort (the stock production models), and if there has been little change in the efforts, then we expect little variability to be explained by the method. All of the five stocks we examined had effort at some times twice as high as at others. In fact some stock production methods always explained some of the variation, but there does not seem to be any relation between the coefficient of varition of efforts and the quality of explanation. If we could find a stock that had no variation in efforts, we would expect to find no forecasting power in the stock production models.

Summary

In this apper we have examined various methods for forecasting short-term changes in catch per unit effort in marine fisheries, based upon historical time series of catches and efforts. We have found that in all stocks good forecasting is quite possible, but the best methods differ from stock to stock. Frequently the stock production models used for long-term management are no better in forecasting next year's CPUE than is the previous year's CPUE. We do not understand the relation between a good short-term forecasting method and an appropriate model for long-term management. That topic is of considerable interest and should be explored in detail. Formal time series methods may be particularly useful.

Acknowledgments

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Box, F. E. P., and G. M. Jenkins. 1970. Time series analysis, forecasting and control. Holden Day, San Francisco, CA. 575 p.

Fox, W. W. Jr. 1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. Fish. Bull. U.S. 73: 23–37.

Gulland, J. A. 1961. Fishing and the stocks of fish at Iceland. U.K. Min. Agric. Fish. Food Fish. Invest. (Ser. 2) 23(4): 52 p.

Hilborn, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. 36: 1477–1489.

Hilborn, R., and M. Ledbetter. 1979. Analysis of the British Columbia salmon purse–seine fleet: dynamics of movement. J. Fish Res. Board Can. 36: 384–391.

Iattc. 1978. Annual report of the Inter-American Tropical Tuna Commission 1977. Inter-Am. Trop. Tuna Comm. Ann. Rep. 1977: 155 p.

Marr, J. C. 1963. A model of the population biology of the Pacific sardine *Sardinops caerulea*. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 154: 270–278.

Mendelssohn, R. 1980. Using Box–Jenkins models to forecast fishery dynamics: identification, estimation and echecking. Fishery Bull. U.S. 78: 887–896.

Pella, J. J., and P. K. Tomlinson. 1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. Bull. 13: 419–496.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

1958. Maximum sustained yields from fluctuating environments and mixed stocks. J. Fish. Res. Board Can. 15: 991–1006.

Saila, S. B., M. Wigbout, and R. J. Lermit. 1980. Comparison of some time series models for the analysis of fisheries data. J. Cons. Int. Explor. Mer 39: 44–52.

Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. 1: 25–56.

1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 2: 245–285.

Schnute, J. 1977. Improved estimates from the Schaefer production model: theoretical considerations. J. Fish. Res. Board Can. 34: 583–603.

Uhler, R. S. 1980. Least squares regression estimates of the Schaefer production model: some Monte Carlo simulation results. Can. J. Fish. Aquat. Sci. 37: 1284–1294.

Walters, C. J., and R. Hilborn. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 143–159.

Westrheim, S. J. [ed.]. 1980. Assessment of groundfish stocks off the west coast of Canada in 1979 and recommended total allowable catches for 1980. Can. Data Rep. Fish. Aquat. Sci. 208: 265 p.

Young, P. 1974. Recursive approaches to time series analysis. Bull. Inst. Math. Appl. 10: 209–224.

Characteristic Size Distributions of Integral Benthic Communities

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SCHWINGHAMER, P. 1981. Characteristic size distributions of integral benthic communities. Can. J. Fish. Aquat. Sci. 38: 1255–1263.

Uniform size spectra comprising bacteria through macrofauna characterize six intertidal communities when biomass concentration is expressed as a function of logarithmic intervals of organism size. Although total community biomass ranged from 70 cm^3/m^2 to 1283 cm^3/m^2, biomass distribution patterns are consistent over the entire size spectrum. Three biomass peaks, at 0.5–1 μm equivalent spherical diameter (29–81 cm^3/m^2), 64–125 μm (0.5–4 cm^3/m^2), and >2 mm (2.4–1283 cm^3/m^2) were separated by typically low biomasses near 8 μm (0–0.04 cm^3/m^2) and 500 μm–1 mm (0–1.5 cm^3/m^2). The peaks correspond to bacteria, interstitial meiofauna, and macrofauna, respectively. Size discontinuities between grain colonizers and interstitial microfauna or epibenthic microflora near 8 μm, and between interstitial meiofauna and burrowing or sedentary macrofauna near 500–1000 μm, are reflected in low biomass values in these size intervals. Comparison of the data with recast published data for other locales shows that similar size distributions characterize a wide variety of benthic communities, including estuarine to abyssal. This study is the first to describe quantitatively, in detail, the size composition of marine benthic communities.

Key words: benthic, community, bacteria, meiofauna, macrofauna, size, biomass, Sheldon spectrum

SCHWINGHAMER, P. 1981. Characteristic size distribution of integral benthic communities. Can. J. Fish. Aquat. Sci. 38: 1255–1263.

Des spectres de taille uniformes allant de bactéries à macrofaune inclusivement caractérisent six communautés intertidales quand on exprime la concentration de biomasse comme fonction d'intervalles logarithmiques de la taille des organismes. Bien que la biomasse totale des communautés varie de 70 cm^3/m^2 à 1283 cm^3/m^2, les caractéristiques de distribution de la biomasse sont uniformes dans le spectre de taille entier. Trois pics de biomasse, de diamètre sphérique équivalent de 0,5–1 μm (29–81 cm^3/m^2), 64–125 μm (0,5–4 cm^3/m^2) et >2 mm (2,4–1283 cm^3/m^2), sont séparés par des biomasses typiquement faibles près de 8 μm (0–0,04 cm^3/m^2) et 500 μm–1 mm (0–1,5 cm^3/m^2). Ces sommets correspondent aux bactéries, à la méiofaune interstitielle et à la macrofaune respectivement. Des discontinuités de taille entre les colonisateurs de grains et la microfaune interstitielle ou microflore épibenthique près de 8 μm, et entre la méiofaune interstitielle et la macrofaune fouisseuse ou sédentaire près de 500–1000 μm se reflètent dans de faibles valeurs de biomasse dans ces intervalles de taille. Une comparaison des données avec celles publiées pour d'autres endroits démontre que des distributions de taille semblables caractérisent une grande variété de communautés benthiques, y compris communautés estuariennes à abyssales. Cette étude est la première à décrire quantitativement, en détail, la composition par taille de communautés benthiques marines.

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PATTERNS of size composition in marine benthic communities were discussed by Thiel (1975) and Gerlach (1978). Their observations were of a general nature, however, and, to date, there has been no quantitative examination of size composition in integral (i.e. including all taxa and sizes of organisms) benthic communities.

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Extensive observations by Sheldon et al. (1972) indicate that size spectra of marine pelagic communities are variations on a simple pattern which is characterized by similar biomass in all logarithmic size-classes of organisms. Further, Sheldon et al. (1972, 1973, 1977) showed that integral community size spectra may be useful comparative measures of community structure and may have predictive value in productivity studies.

Kerr (1974) and Silvert and Platt (1978) examined these

results in terms of energy transfer models wherein size-dependent metabolism and predation determine community size composition. Their models suggest that size compositions of pelagic communities are constrained within definite, predictable patterns. But can their reasoning be extended to benthic communities?

Smith (1976) argued that although food-web interactions constitute the only organizing force in open-water communities, a second organizing force, competition for space, is present in communities inhabiting a stable surface. A consequence, he reasoned, would be that open-water and surface-dwelling communities exhibit different distributions of fast (small, *r*-selected) and slow (large, *K*-selected) species. Thus, we expect to find consistent patterns in benthic community size spectra, but the patterns and their associated dynamics may be more complex than the models of Kerr and Silvert and Platt predict.

Kerr (1976) perceived size composition to be an emergent property of integral biological communities; characteristic patterns occur in communities with similar dynamics irrespective of their taxonomic composition. Size composition cannot supplant taxonomic description as a measure of community structure, but the two can be complementary in comparative studies of community ecology, productivity, and biotic and environmental interactions in intact communities.

Sheldon et al. (1972) introduced to ecology a useful graphical representation of community size composition, which I shall refer to as the Sheldon spectrum. Originally used to describe Coulter counter particle size distributions, it is a plot of particle concentration, by volume, against particle diameter. Particle diameter of a nonspherical organism is calculated as the diameter of a sphere of equal volume. Total concentration of all organisms in each logarithmic (base 2) size interval regardless of species classification is plotted against this equivalent spherical diameter.

Observations on the Sheldon spectra of six intertidal benthic communities in Nova Scotia and New Brunswick are presented here. Literature data, derived from a variety of benthic communities, have been recast to provide a more extensive, if approximate, sampling of the Sheldon spectra in the marine benthos. This represents the first use of the Sheldon spectrum to characterize benthic communities.

Study Sites

Peck's Cove, New Brunswick

Peck's Cove is an extensive silt flat at the mouth of the Cumberland Basin in the upper Bay of Fundy (Fig. 1). The tidal range is over 12 m. Exposed flats extend out ~1 km at low tide. Two sampling stations were established. Station A, in the upper intertidal zone near the edge of a *Spartina* fringe, is inundated for 3–4 h of each semidiurnal tidal cycle. Station B, 800 m out from station A and ~100 m from mean low water, is inundated for 9–10 h of each tidal cycle. Both stations have fluid (~50% water content) silt–clay surface sediments of low organic content (0.8% C) overlying a more compact sandy silt substrate at variable depth, usually 5–20 cm, below the surface. Surface sediment at station A is stable during the ice-free season, but at station B it is subject to frequent and sometimes extensive shifting, up to 20 cm in a 2-wk period. Ice scouring occurs at both stations from January through March. Both stations were sampled on May 5, 1979.

Petpeswick Inlet, Nova Scotia

Petpeswick Inlet is an embayment on the Atlantic coast of Nova Scotia (Fig. 1). The inner reaches are estuarine, with a tidal range of less than 2 m. Station 27/1 is a highly organic 19% C) mud flat (29% silt–clay) in the sheltered inner basin of the Inlet. Samples were collected from 27/1 in two parallel transects from low tide level to the upper intertidal zone on January 27, 1979. The other Petpeswick sites, near the mouth of the Inlet, have a tidal range of 3 m. Station 26/1 is a sand flat with low organic (1.2% C) and silt–clay (0.8%) content. Stations 29/12 and 30/12 are separated from 26/1 and sheltered by a stone jetty. Station 29/12 has lower organic (1.7% C) and silt–clay (9%) content than station 30/12 ((5.9% C, 49% silt–clay) which receives domestic septic seepage. Samples were collected at 15-m intervals in transects normal to the shoreline from low tide level to the upper intertidal zone at each site. Stations 29/12 and 30/12 were sampled on December 29 and 30, 1978; station 26/1 was sampled on January 26, 1979.

Materials and Methods

Macrofauna were sampled at low tide with a 98- or 198-cm^2 PVC corer to a depth of 30 cm. The total area sampled at each site was adjusted to obtain adequate numbers of the largest obvious macrofaunal organisms and ranged from 0.1 m^2 at Peck's Cove stations A and B (5 × 198 cm^2 at each station) to 0.5 m^2 at Petpeswick Inlet 26/1 (25 × 198 cm^2). Material was preserved in 2.5% glutaraldehyde–seawater and sieved onto 420-μm mesh. Organisms were sorted by taxa and approximate size groups. Volumes of individuals, or groups of similarly sized individuals of the same taxonomic group, were measured by volume displacement in suitably sized pipettes or graduated cylinders.

Meiofauna, including protozoa, and microalgae were collected to a depth of 10 cm adjacent to the macrofauna samples with 5.5-cm^2 plastic coring tubes. Organisms were relaxed with 7% $MgCl_2$, fixed in 1% glutaraldehyde–seawater, separated from the sediment by centrifugation in a silica sol, and collected on a 10-μm mesh screen placed on a vacuum filtration apparatus (Schwinghamer 1981). They were rinsed into 25-cm^3 settling chambers, enumerated, and measured using an inverted plankton microscope with calibrated ocular grid. Volumes were calculated from geometrical figures closely approximating the shapes of the organisms.

Whole sediment samples were collected in 0.09-cm^3 aluminum sample boats at 0, 5, and 10 cm depth for bacterial counts. They were fixed in filtered 2.5% glutaraldehyde–seawater and stored frozen prior to enumeration using the epifluorescence technique of Hobbie et al. (1977). Size distributions of microbial populations were obtained by measuring all cells and filaments up to and including 10 μm minimum

FIG. 1. Sampling locations at Peck's Cove, N.B., and Petpeswick Inlet, N.S. Broken lines indicate low tide level.

dimension in a random selection of fields in each sample.

Organism volumes (V) were converted to equivalent spherical diameter (D) by the formula $D = 2\sqrt[3]{\frac{3V}{4\pi}}$. The total biomass of each $\log_2$ size-class is expressed as volume (cm^3)/sediment surface area (m^2). Log_2 size intervals are convenient to work with and coincide with Sheldon et al. (1972) size intervals, yet provide much better resolution of the size spectrum that do $\log_{10}$ intervals. Because biomass estimates of bacteria, microalgae, and meiofauna were made to 10 cm depth, and most macrofauna occurred in the top 10 cm, 1 cm^3/m^2 is equivalent to a concentration of 10 cm^3/m^2 or 10 ppm.

Additional data were obtained from the published literature. Warwick et al. (1979) gave numbers of individuals and carbon biomass of each taxon over the entire size spectrum in the Lynher Estuary, U.K. Sanders (1960) and Wieser (1960) gave numbers of individuals of meio- and macro-fauna in Buzzard's Bay, MA, but expressed biomass as dry weight. Wigley and McIntyre (1964) provided similar data on a number of New England shelf and slope stations. I have used only their extreme values (stations 46 and 55) to indicate the range they encountered. I have estimated biomass of size-classes in three shallow Baltic Sea stations from histograms of wet weight biomass versus weight-class given by Fenchel (1969). His data cover a weight range of 10^{-9} to 10 g. Data from Thiel (1975), Gerlach (1978), and Ankar (1979) represent only very approximate average size-classes in the bacteria, micro-, meio-, and macro-fauna. I have used the maximum and minimum deep-sea biomass values given by Thiel. Ankar's data are from the Asko area of the Baltic Sea. Gerlach's figures are of a more speculative nature, being representative of a hypothetical 30-m sandy bottom station.

Biomass data derived from these literature sources were converted to volume by assuming wet weight (g) = volume (cm^3), dry weight = 0.25 wet weight, and carbon = 0.1 wet weight. Mean body volume per individual was calculated for each taxon by dividing total taxon biomass by number of individuals unless sizes were specifically stated by the authors. This method does not account for the range of sizes possible in each taxon, but provides a first approximation of community size structure.

TABLE 1. Biomass values of size-classes of organisms in benthic communities at Petpeswick Inlet, Nova Scotia, and Peck's Cove, New Brunswick. Figures in parentheses under biomass total are standard errors of the mean of replicate samples. Coefficient of variation = $100 \times \frac{\text{standard deviation}}{\text{mean}}$.

	Size-class (equivalent spherical diameter)	Unit area biomass (cm^3/m^2)							
		Peck's Cove		Petpeswick Inlet					Coefficient of variation (%)
		A	B	29/12	30/12	26/1	27/1	Mean	
"Bacteria"	0.5 μm	25	28	37	44	29	81	41	51
	1	30	28	15	79	12	50	36	70
	2	7.5	4.6	0.37	0.50	0.29	3.4	2.8	106
	4	0.51	0.42	0.16		0.13	0.7	0.32	76
	Total	63.1 (2.7)	61.0 (2.7)	52.5 (6.4)	123.5 (4.8)	41.4 (1.6)	135.1 (10.8)	80.1	
"Microalgae, meiofauna"	8 μm	0.03	0.04					0.012	157
	16	0.31	0.04	0.15		0.11	0.14	0.12	94
	32	1.2	0.13	1.6	0.63	0.88	1.2	0.94	50
	64	0.92	0.87	2.6	2.6	0.53	2.2	1.6	58
	125	2.0	1.9	4.1	4.0	0.48	1.8	2.4	59
	250	0.29	0.34	1.3	1.2	0.41	0.70	0.71	63
	500	0.23	1.1	0.18	0.08	0.15	0.13	0.32	125
	Total	5.0 (0.19)	4.4 (0.17)	9.9 (0.45)	8.5 (2.6)	2.6 (0.23)	6.2 (1.1)	6.1	
"Macrofauna"	1 mm		0.81	0.38		1.5	0.50	0.53	107
	2	2.1	2.4	1.1	0.14	0.57	8.2	2.4	122
	4	14	1.5	72	57	5.2	20	28	94
	8	17		11	530	4.0	4.4	94	226
	16				563	117	940	270	146
	32			85		168		42	167
	Total	33.1 (7.3)	4.7 (1.0)	169 (52)	1150 (298)	296 (78)	973 (697)	473	
Total		101	70	223	1283	341	1114	536	

Results[1]

PECK'S COVE, N.B.

Total biomasses per unit area were similar at stations A and B, and were the lowest values encountered in the six sampling locations (Table 1). Similar biomasses of bacteria dominated the communities at both stations, contributing 62% of the total biomass at station A and 87% at station B. Microalgae and meiofauna including protozoa comprised the 8- to 500-μm size-classes accounting for only 5.0 and 6.3% of the total biomass at stations A and B, respectively. Nematodes, primarily in the 64- and 125-μm size-classes, dominated the meiofauna at station A. Testate Foraminiferida dominated the meiofauna at station B. Fewer epibenthic diatoms at station B resulted in lower biomass in the 16- and 32-μm size-classes than at station A. The polychaete *Aglaophamus circinata* was abundant in the 0.5- and 1-mm size-classes at station B. At station A, *Aglaophamus* did not occur, but oligochaetes of 0.5-mm size-class were present.

Most of the biomass difference between the two stations was attributable to the macrofauna (Table 1). *Heteromastus filiformis* and *Macoma balthica* accounted for 90% (30 cm^3/m^2) of the marcofaunal biomass at station A. *Macoma* did not occur and *Heteromastus* was not abundant at station B. The biomass of *Corophium volutator* was similar at both stations. No large macrofauna (16- and 32-mm size-classes) were sampled at either Peck's Cove station.

The standard errors of the biomass estimates of bacteria, microalgae, and meiofauna are small (Table 1) and even the relatively larger errors associated with the macrofauna biomass estimates are not large enough to affect the interpretation of the data.

PETPESWICK INLET, N.S.

Total biomasses per unit area at all four Petpeswick stations were higher than those at the Peck's Cove stations (Table 1). Sampling precision at the Petpeswick sites, as indicated by

[1]A complete set of tabular data on size distribution of taxonomic groups is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

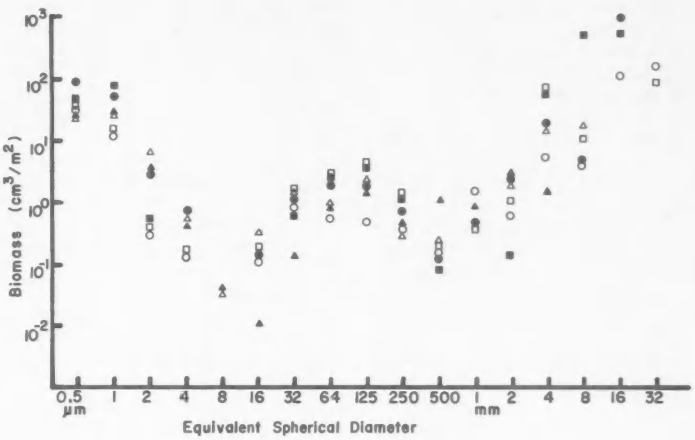

FIG. 2. Sheldon spectra of the six intertidal sampling locations. Peck's Cove station A, △; station B, ▲. Petpeswick 29/12, □; 30/12, ■; 26/1, ○; 27/1, ●.

standard error, is given in Table 1. The macrofauna estimate at Petpeswick 27/1 is the only value whose standard error is greater than about 25% of the mean.

Bacteria did not dominate the biomass at any Petpeswick station, accounting for only 10−23% of the total. Bacterial biomasses of the two more highly organic stations, 30/12 and 27/1, exceeded those of the sandy stations, 29/12 and 26/1, roughly by a factor of 2.5, but were only about 25−30% higher than the Peck's Cove values.

Although the relative contributions of taxonomic groups in the 8- to 500-µm size-classes were not consistent among the four sites, total biomasses in this range were of the same order of magnitude as the Peck's Cove values (Table 1). The meiofauna at station 26/1 was not dominated by any one group, there being similar biomasses of protozoans, nematodes, and small annelids. Nematodes dominated the meiofauna at the other stations. As at Peck's Cove, epibenthic diatoms dominated the 16- to 64-µm size range. No organisms in the 8-µm size-class were observed at any of the Petpeswick stations.

In contrast with the Peck's Cove stations, all four Petpeswick stations were dominated by macrofauna, which contributed 73−90% of the total biomass. But, as was the case at Peck's Cove, almost all the variation in biomass among the Petpeswick sites was attributable to the macrofauna. The lowest macrofaunal biomass among the Petpeswick sites (169 cm^3/m^2) was at station 29/12, where patches of *Mytilus edulis* and *Clymenella torquata* codominated the community. The other low biomass station, 26/1, was dominated by *Mya arenaria* which accounted for 85% (290 cm^3/m^2) of the total community biomass. Both of the high biomass stations, 30/12 and 27/1, were dominated by *Mytilus edulis*, which accounted for 81 and 84%, respectively, of the total community biomass. Unlike stations 29/12 and 26/1, neither 30/12 nor 27/1 had organisms in the 32-mm size-class.

COMPARISON OF THE SHELDON SPECTRA

Figure 2 illustrates the data for the six sampling locations at Peck's Cove and Petpeswick Inlet as Sheldon spectra. The most obvious common features of the spectra are biomass peaks in the smallest (<2-µm) and largest (>2-mm) size-classes and a lesser peak at 32- to 125-µm equivalent spherical diameter. These peaks are separated by regions of generally low (<1 cm^3/m^2) biomass in the 4- to 16-µm and 500-µm to 1-mm size-classes. Reexamination of the samples confirmed that these "troughs" are not methodological artifacts.

The magnitude of the peak associated with bacteria was 30−80 cm^3/m^2 at the lower end of the size scale. The logarithmic ranges of values in the 0.5- to 2-µm classes were narrow but increased as the spectrum approached the 4- to 16-µm trough.

In the 32- to 500-µm size-classes the ranges of values were again narrow. At all locations except 26/1, the biomass peaked at 2−4 cm^3/m^2 in either the 64- or 125-µm size-class. The peak at 26/1 was 0.88 cm^3/m^2 in the 32-µm class. There was another peak at this station, not present at the others, of 1.5 cm^3/m^2 in the 1-mm size-class. There was a general trend among the stations to lower biomass (<1 cm^3/m^2) in the 0.5- and 1-mm size-classes. Very few, if any, organisms at Peck's Cove station A or Petpeswick 30/12 occurred in the 1-mm size-class on the sampling dates although larvae of many macrofaunal species pass through this size-class during growth, possibly later in the season.

The macrofaunal size range was the most variable part of the spectrum (Table 1), especially the 8- to 32-mm size-classes, whose biomasses ranged from 0 to 940 cm^3/m^2. The trend of the spectrum was that the highest biomass occurred near the largest class.

Comparison of the means and ranges of biomass values obtained in this study with representative literature values in

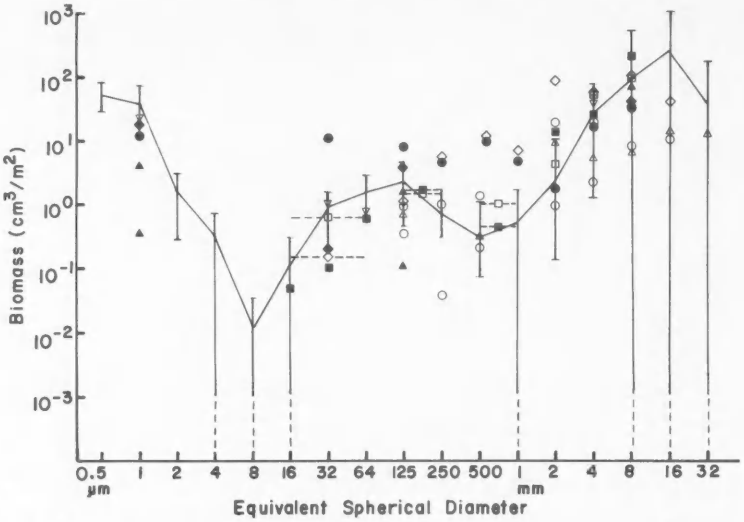

FIG. 3. Average Sheldon spectrum and ranges of values of the six sampling locations. Symbols indicate literature-derived values: Sanders (1960) and Wieser (1960), △; Wigley and McIntyre (1964), ○; Fenchel (1969) and Nivå Bay, ◇; Ålsgård, ■; Helsingør, □; Thiel (1975), ▲; Gerlach (1978), ◆; Ankar (1979), ▽; Warwick et al. (1979), ●.

Fig. 3 shows that the same characteristic Sheldon spectrum is typical of a wide variety of benthic communities. It must be stressed, however, that the literature values are approximations extracted from data collected and analyzed for other purposes. Only Warwick et al. (1979) include microalgae in their data. No size data are available in these community studies for the 0.5- to 8-μm classes. A conspicuous feature of most of the data is the very low biomass of the 0.5- or 1-mm size-classes. Warwick et al. (1979) caution that this may be due to methodological errors, but at least at Peck's Cove and Petpeswick Inlet it was not an artifact. Biomass values much greater than 1 cm^3/m^2 in these size-classes occurred only in the Lynher Estuary (Warwick et al. 1979) and Nivå Bay (Fenchel 1969).

Discussion

The coherent pattern of the Sheldon spectra exhibited by the six intertidal communities examined in this study and its close fit to data from other marine benthic communities suggest that a general theory of benthic community size structure may be possible. It is not directly obvious why the Sheldon spectrum for these benthic communities shows the pattern it does, so I shall examine some factors which may determine its form.

Typical features of the benthic Sheldon spectrum are (1) biomass maxima at the lower and upper extremes of the size scale, (2) a local maximum, one to three orders of magnitude less than the others, at the center of the size spectrum, (3) local biomass minima at 4−16 μm and 0.5−1 mm, and (4) truncation of the size spectrum in the range of 8−64 mm. The position of the spectrum on the biomass ordinate is of fundamental interest as an integral function of energy input into benthic communities. It is noteworthy that the mean biomass per unit area of the 0.5- to 125-μm size range in the six intertidal benthic stations (86 cm^3/m^2) is of the same order of magnitude as an integrated unit area pelagic biomass (1−100 μm) typical of North Atlantic and South Pacific open ocean stations (125−200 cm^3/m^2, from Sheldon et al. 1972, Fig. 10C).

The Structure of Marine Sediments; Microscopic and Macroscopic Surfaces

Marine sediments comprise two phases whose boundary depends upon the physical scale of definition. At a macroscopic scale, the overlying water grades into increasingly compact sediment which is very fluid at its surface, more solid at depth. At a microscopic scale the phases are more distinct, with well-defined solid particles in an aqueous medium, their concentration increasing with depth in the sediment. The "surface" of the sediment occurs at two scales, so the evolutionary constraints and advantages contingent upon sedentary surface dwellers proposed by Smith (1976) also occur at two scales.

The two biomass peaks at the extremes of the size scale both represent surface dwellers, the larger ones at the macroscopic mud−water interface and the smaller on microscopic sediment grain surfaces. As Smith pointed out, where a habitable surface exists and nutrients and energy are passively dispersed in the environment, sedentary surface dwellers have an advantage over mobile forms in that they can elaborate

food gathering and protective devices that would impede locomotor ability. He argued that in such systems, most of the biomass soon becomes locked up in large, long-lived species at the basal trophic level (whose energy source is external to the community). These are the "matrix" species of the surface community whose presence adds a secondary biogenic, structure to the physical habitat (Paine 1976). At a microscopic scale, sediment grain communities are dominated by bacterial or algal colonies whose size may be controlled by similar factors at a different scale.

Microscopic and Macroscopic Surface Dwellers

The Sheldon spectra indicate that bacterial biomass in marine sediments, including deep ocean areas, is likely to exhibit less than two orders of magnitude variation. Bacterial populations in different communities appear to have similar size distributions, with a biomass peak in the 0.5- to 1-μm size-classes and an upper limit in the 4-μm size-class. I do not imply that bacterial activity should be similar in all benthic communities, but only that as community structural features, bacterial biomass and size distribution vary within narrow limits.

Hargrave (1972) and Hargrave and Phillips (1977) showed that microbial oxygen consumption in sediments is related to both particle surface area and concentration of organic matter. My results support this conclusion, the highest microbial biomass being in organic silt−sand sediments (Petpeswick 30/12, 27/1), the lowest in organic-poor sand (Petpeswick 29/12, 26/1). Intermediate values were found at Peck's Cove, with finer sediments but the lowest organic content. The percent sediment <64 μm (an index of particle surface area) and percent carbon in the sediment taken together correlated well with bacterial biomass ($r^2 = 0.96$) whereas independently they were neither correlated themselves nor with bacterial biomass. Thus, although bacterial numbers and activity may be influenced by biological interactions (e.g. Hylleberg 1975; Tenore 1977; Gerlach 1978) the net effect is that they are limited primarily by habitable grain surface, and the quality and rate of influx of organic matter.

All macrofauna are dependent upon events at the macroscopic sediment surface for their existence. They require contact with the surface, either constantly or periodically, directly or indirectly through biogenic structures and sediment reworking. Food influx occurs largely as a surface phenomenon, so in the sense of Smith (1976), both suspension and deposit feeders are ultimately limited by space at the sediment surface. Accordingly, benthic communities should be dominated by the largest "matrix" species permitted by the climate at the surface.

The absence of the larger size-classes at Peck's Cove is almost certainly a result of physical factors and is especially noticeable at station B. Winter ice scouring decimates populations of perennial species such as *Macoma* at both stations, but apparently less so at station A. Continuous and often extensive sediment shifting during the ice-free season at station B restricts the macrofauna to small opportunists such as *Corophium* and *Aglaophamus*. Station A is more stable during this time so larger populations of the more sedentary *Heteromastus* and *Macoma* can develop. Petpeswick stations 30/12 and 27/1 both have very high biomass, but their size spectra are truncated above the 16-mm size-class. The truncation is probably caused by crowding, i.e. space limitation (both stations are mussel beds), combined with environmental disturbances of sufficient frequency to prevent the existence of old populations and thus larger individuals. Food does not appear to be a size-limiting factor in these rich organic sediments.

Food supply may not limit the maximum extent of the size spectrum, but reduced organic input may limit total community biomass. Although larger individuals are present at Petpeswick stations 29/12 and 26/1, these stations have much lower macrofaunal biomass than stations 30/12 and 27/1, which have much higher organic content and bacterial populations. The Peck's Cove stations, both with very low organic content, have the lowest macrofaunal biomasses in spite of moderately large bacterial populations associated with the large surface area in these fine-grained sediments.

The Interstitial Meiofauna

The local biomass maximum between 32 and 250 μm is associated with interstitial meiofauna. These organisms, not being surface dwellers, probably are not space limited in the sense of Smith. Hulings and Gray (1976) concluded that pore space plays a minor role in determining meiofaunal abundance. But pore space and grain size probably determine the upper and lower size limits of the interstitial fauna and thus the characteristic biomass troughs of the benthic Sheldon spectrum.

A biomass minimum in the 4- to 16-μm size range separates the mobile interstitial biota from the microscopic grain surface dwellers. The minimum could be a result of both evolutionary and ecological factors. Smaller size would be consistent with sedentary life as a grain dweller, affording the individual greater protection in the concavities of sediment particles and allowing for more rapid growth (by the r_{max}−size relationship of Fenchel 1974) of colonies on newly arrived food sources. No grain-surface dwellers were observed in the 8- or 16-μm size-classes, the populations in this size range consisting largely of phytoflagellates and diatoms. Cropping is likely to be heavy in the 4- to 16-μm size range, an 8-μm organism being a suitably sized food item for a raptorial free-living organism in the 64- to 125-μm size-classes, or a larger macrofaunal filter feeder. Notably, there are no active fauna smaller than the 32-μm size-class at any of the study sites. The meiofauna thus avoid the size ranges that are very heavily cropped. They reach peak biomass in those size ranges for which 4- to 16-μm organisms are suitably sized individual food items (Kerr 1974).

A biomass minimum in the 500-μm to 1-mm size-classes of most benthic Sheldon spectra defines the upper limit of the interstitial meiofauna. Fenchel (1969) noted that this is a region of shift in lifestyle from interstitial to burrowing and sedentary macroscopic surface dwelling. Interstitial organisms must be considerably smaller than the median particle size in order to move about freely, whereas burrowers such as large nematodes and smaller macrofauna must be larger to avoid entrapment by sediment particles. For interstitial forms to exist in very fine sediments such as at Peck's Cove, the

water content must be high enough (40% at Peck's Cove) to permit the existence of interstices substantially larger than the sediment particles.

Interstitial organisms are adapted to move in an environment of low Reynolds number, a maze of tunnels filled with viscous fluid (water), where the effort required of an organism to overcome its own inertia is much less than that required to overcome viscosity of the medium. Because they are equipped to overcome viscous rather than inertial force, interstitial organisms cannot exist in an environment in which they must displace large (to them) particles in order to move.

Infauna that are much larger than sediment particles also experience life at low Reynolds number in the viscous mixture of water and solid particles of the soft bottom. They have adapted to life in a viscous fluid by generally reducing their motility, often by building permanent or semipermanent structures within which they move only to a limited extent. Sedentary or generally slow-moving suspension and deposit feeders are the dominant trophic types among the macrofauna (Gray 1974). Active carnivores and omnivores live as epifauna or in the very fluid sediment surface (Jumars and Fauchald 1977).

Between the interstitial fauna and the macrofauna lie the size-classes in which organisms are restricted by dimensions of sediment interstices. Organisms in these size-classes, usually 500 μm to 1 mm, are probably restricted to the very fluid surface of most sediments where, in fact, they function as interstitial forms, but like macrofauna are limited by surface space. The abundance of organisms in this size range in the Lynher Estuary (Warwick et al. 1979), Nivå Bay (Fenchel 1969), and, to some extent, Peck's Cove station B is probably due to the greater than normal depth of very fluid sediments at these stations. One would also expect to find these size-classes in abundance in coarse sediments such as the coarse sand of Petpeswick 26/1.

Because interstitial organisms probably are not space limited, their rapid rates of reproduction relative to the macrofauna, predicted by the r_{max}–size relationship (Fenchel 1974), could result in higher biomass levels than observed, especially in areas of high organic content. But the Sheldon spectra indicate that meiofaunal biomass is a conservative feature of benthic communities.

It is generally believed that meiofauna use food resources that are also part of the diet of macrofaunal deposit feeders (e.g. Tenore 1977; Warwick et al. 1979). However, as Gerlach (1978) argued, and experimental studies suggest (Tenore et al. 1977; Hylleberg 1975), the nature of the interaction between the two groups is more complex than merely resource competition. Recent observations suggest that meiofauna may be an important food source not only for infauna (Elmgren 1976, 1978; Reise 1979) but for benthic feeding epifauna as well (Elmgren 1976; Buzas 1978; Sibert 1979). A dynamic balance is most likely maintained between positive and negative size-dependent interactions in the infauna. This is reflected in the relatively invariant magnitude of the meiofauna peak.

Conclusion

The Sheldon spectrum is a useful, practical tool of ecology. Details of the spectrum can be used as bases of comparison among communities and, as I have attemtped here, to frame hypotheses concerning dynamics that may affect community structure. If a typical spectrum can be described, then variance from the typical pattern might be examined as a means to discover the effects of exogenous distrubance. Such an application may be useful in environmental impact and pollution studies.

A particularly beneficial application of the Sheldon spectrum would be to survey benthic productivity. Using the empirical physiological approach of Peters (1978), Sheldon spectra may be integrated with size-dependent metabolic functions such as those describing respiration and *P/B* ratio given by Banse (1979) to give good approximations of community respiration and production. As an example, I calculated macrofaunal production in the Lynher Estuary using Banse's size–*P/B* relationship and size spectrum data derived from Warwick et al. (1979). Banse's equation, $\log Pa/B = -0.19 - 0.37 \log Ws$ (Pa = cumulative annual production, B = mean annual biomass, Ws = body mass at maturity, all units are kilocalories (1 cal = 4.188 J)), was derived from measurements with macrofaunal-sized organisms and cannot be applied to size-classes smaller than 1 mm. Calculated in this way, the total macrofaunal production in the Lynher estuary is 9.6 g $C \cdot m^{-2} \cdot yr^{-1}$. This compares with an estimate of 5.46 g $C \cdot m^{-2} \cdot yr^{-1}$ obtained by Warwick et al. by summation of production by the most abundant macrofaunal species. It is impossible to define the confidence interval of either figure, but considering the large numbers of assumptions, approximations, and sources of error involved in the usual production calculations, the two figures are likely in agreement. With improved versions of the size-*P/B* relationship based on a wider size range of organisms, such calculations could estimate community production for all sizes of organisms with far less effort than is at present necessary to obtain production estimates.

Acknowledgments

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ANKAR, S. 1979. Annual dynamics of a northern Baltic soft bottom. *In* E. Naylor and R. G. Hartnoll [ed.] Cyclic phenomena in marine plants and animals. Pergamon Press, New York, NY.

BANSE, K. 1979. On weight dependence of net growth efficiency and specific respiration rates among field populations of invertebrates. Oecologia 38: 111–126.

BUZAS, M. A. 1978. Foraminifera as prey for benthic deposit feeders; results of predator exclusion experiments. J. Mar. Res. 36: 617–625.

ELMGREN, R. 1976. Baltic benthos communities and the role of the meiofauna. Contrib. Asko Lab. Univ. Stockholm 14: 1–31.

1978. Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro and meiofauna. Kiel. Meeresforsch. Sonderheft 4: 1–22.

FENCHEL, T. 1969. The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to ciliated Protozoa. Ophelia 6: 1–182.

1974. Intrinsic rate of natural increase: the relationship with body size. Oecologia 14: 317–326.

GERLACH, S. 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia 33: 55–69.

GRAY, J. S. 1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Annu. Rev. 12: 223–261.

HARGRAVE, B. T. 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. Limnol. Oceanogr. 17: 583–596.

HARGRAVE, B. T., AND G. A. PHILLIPS. 1977. Oxygen uptake of microbial communities on solid surface, p. 547–587. *In* J. Cairns [ed.] Aquatic microbial communities. Garland Publishing, New York, NY.

HOBBIE, J. E., R. J. DALEY, AND S. JASPER. 1977. Use of nucleopore filters for counting bacteria by fluorescence microscopy. Appl. Environ. Microbiol. 33: 1225–1228.

HULINGS, N. C., AND J. S. GRAY. 1976. Physical factors controlling abundance of meiofauna on tidal and atidal beaches. Mar. Biol. 34: 77–83.

HYLLEBERG, J. 1975. Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. Ophelia 14: 113–137.

JUMARS, P. A., AND K. FAUCHALD. 1977. Between-community contrasts in successful polychaete feeding strategies, p. 1–20. *In* B. C. Coull [ed.] Ecology of marine benthos. University of South Carolina Press, Columbia, SC.

KERR, S. R. 1974. Theory of size distribution in ecological communities. J. Fish. Res. Board Can. 31: 1859–1862.

1976. Ecological analysis and the Fry paradigm. J. Fish. Res. Board Can. 33: 329–332.

PAINE, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus–Pisaster* interaction. Ecology 57: 858–873.

PETERS, R. H. 1978. Empirical physiological models of ecosystem processes. Int. Ver. Theor. Angew. Limnol. Verh. 20: 110–118.

REISE, K. 1979. Moderate predation on meifauna by the macrobenthos of the Wadden Sea. Helgol. Wiss. Meeresunter. 32: 453–465.

SANDERS, H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. Limnol. Oceanogr. 5: 138–153.

SCHWINGHAMER, P. 1981. Extraction of living meiofauna from marine sediments by centrifugation in a silica sol–sorbitol mixture. Can. J. Fish. Aquatic Sci. 38: 476–478.

SHELDON, R. W., A. PRAKASH, AND W. H. SUTCLIFFE JR. 1972. The size distribution of particles in the ocean. Limnol. Oceanogr. 17: 327–340.

SHELDON, R. W., W. H. SUTCLIFFE JR., AND M. A. PARANJAPE. 1977. Structure of pelagic food chain and relationship between plankton and fish production. J. Fish. Res. Board Can. 34: 2344–2353.

SHELDON, R. W., W. H. SUTCLIFFE JR., AND A. PRAKASH. 1973. The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. Limnol. Oceanogr. 18: 719–733.

SIBERT, J. R. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary: II. Meiofauna available as food to juvenile chum salmon. J. Fish. Res. Board Can. 36: 497–503.

SILVERT, W., AND T. PLATT. 1978. Energy flux in the pelagic ecosystem: a time-dependent education. Limnol. Oceanogr. 23: 813–816.

SMITH, F. E. 1976. Ecosystems and evolution. Bull. Ecol. Soc. Am. Spring 1976: 2–6.

TENORE, K. R. 1977. Food chain pathways in detrital feeding benthic communities: a review, with new observations on sediment resuspension and detrital recycling, p. 37–53. *In* B. C. Coull [ed.] Ecology of marine benthos. University of South Carolina Press, Columbia, SC.

TENORE, K. R., J. H. TIETJEN, AND J. J. LEE. 1977. Effect of meiofauna on aged eelgrass *Zostera marina* detritus by the polychaete *Nephthys incisa*. J. Fish. Res. Board Can. 34: 563–567.

THIEL, H. 1975. The size structure of the deep-sea benthos. Int. Rev. Gesamten Hydrobiol. 60: 575–606.

WARWICK, R. M., J. R. JOINT, AND P. J. RADFORD. 1979. Secondary production of the benthos in an estuarine environment, p. 429–450. *In* R. L. Jeffries and A. J. Davy [ed.] Ecological processes in coastal environments. Blackwell Scientific Publications, London.

WIESER, W. 1960. Benthic studies in Buzzards Bay. II. The meiofauna. Limnol. Oceanogr. 5: 121–137.

WIGLEY, R. L., AND A. D. MCINTRYE. 1964. Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. Limnol. Oceanogr. 9: 485–493.

Prey Location Volume of a Planktivorous Fish: A New Measure of Prey Vulnerability

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LUECKE, C., AND W. J. O'BRIEN. 1981. Prey location volume of a planktivorous fish: a new measure of prey vulnerability. Can. J. Fish. Aquat. Sci. 38: 1264–1270.

The probability that bluegills (sunfish) (*Lepomis macrochirus*) will locate prey varies with distance and position of the prey in three-dimensional space. Location ability is greatest in the hemisphere directly ahead of the fish. The probability that bluegills will locate prey declines steadily when prey are placed to the side, behind, or directly above or below the fish. Bluegills could locate prey farthest when placed slightly to the side of the area directly in front of the fish. Under all experimental conditions, fish could locate prey, at least some of the time, at distances considerably farther than suggested by reported reactive distance measurements, indicating that the water volume searched by bluegills has generally been underestimated.

Key words: planktivorous fish, zooplankton, reactive distance, location volume, predator search

LUECKE, C., AND W. J. O'BRIEN. 1981. Prey location volume of a planktivorous fish: a new measure of prey vulnerability. Can. J. Fish. Aquat. Sci. 38: 126[4]–1270.

La probabilité que les crapets arlequins (*Lepomis macrochirus*) sont capables de localiser leur proie varie en fonction de la distance et de la position de cette dernière dans un espace tridimensionnel. La capacité de localisation est maximale dans l'hémisphère directement en avant du poisson. La probabilité que les crapets pourra localiser sa proie diminue régulièrement quand cette dernière est placée à côté, en arrière ou directement au-dessus ou au-dessous du poisson. Les crapets arlequins peuvent localiser leurs proies à de plus grandes distances quand ces dernières sont placées légèrement à côté de la région directement en avant du poisson. Dans toutes les conditions expérimentales, les poissons ont pu localiser leur proie, au moins quelques fois, à des distances beaucoup plus grandes que celles suggérées par des mesures déjà publiées de la distance de réaction, ce qui laisse supposer que le volume d'eau prospecté par les crapets arlequin a généralement été sous-estimé.

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THE predator–prey interaction between planktivorous fish and zooplankton is a finely tuned system in which each party appears to have stretched its adaptive capacity to the maximum. Zooplankton, in their small size, transparency, and ability to migrate to dark areas during the day (Zaret 1972; Zaret and Suffern 1976; Zaret and Kerfoot 1975; O'Brien et al. 1979) have made search a key to planktivorous fish-feeding ecology (O'Brien 1979).

In most previous work on searching of planktivorous fish for prey, the reactive distance approach of Holling (1959) as applied to fish by Ware (1973), has been used. In reactive distance studies, fish are commonly trained to cruise over long narrow aquaria in search of food. The investigators then arbitrarily place zooplankton prey along the path and record the distance from the prey that the fish "reacts" (commonly described as a slight hesitation with binocular fixation on the prey and then a rapid attack on the prey) (Werner and Hall 1974; Confer and Blades 1975; Vinyard and O'Brien 1976; D. Schmidt and W. J. O'Brien 1981). However, in nature planktivorous fish must search a large three-dimensional volume of water, not just the area directly in front of them. Confer et al. (1978) first investigated the three-dimensional reactive volume of a planktivorous fish and found an overall reduction in the distance at which lake trout reacted to prey.

We wished to expand and extend the analysis of search volume using a centrarchid planktivore, the bluegill (sunfish) (*Lepomis macrochirus*). We therefore trained bluegills to enter a small opaque enclosure within a large cubic aquarium and, when the enclosure door was opened, to search the entire area for prey. This method enabled us to describe the full volume within which bluegills locate prey and to determine the probability of prey being seen at any point.

Methods

Bluegills 5–9 cm TL, were seined from a nearby pond and held in small stock tanks prior to experiments. Only four fish

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were used as we have found variability between individual fish to be very small. For example, Werner and Hall (1974), Confer and Blades (1975), and Vinyard and O'Brien (1976) all reported the same reactive distance values for bluegills feeding at high light intensity on similar sized prey. Measurements of reactive volume were made in four vertical planes (0° or forward-directed, 45°, 90°, 135°) and the horizontal plane at approximately fish eye level (0°).

For experiments in the vertical plane, we used a large square aquarium (90 × 90 × 60 cm) within which was a wedge-shaped enclosure for the fish. A set of polar coordinates was suspended along one wall. Fish were trained to enter the enclosure, turn to face forward, and search the tank for prey when the enclosure door was opened. Prey, 2-mm *Daphnia magna*, were introduced with a long syringe into the tank and placed at the center of the measurement grid while the fish was inside the enclosure. The site of the prey at the moment the enclosure door opened was recorded as the coordinates of the grid, which was defined by 1-cm contours and 10° radians. Thus, prey recorded as 20 out and 40 up was 20 cm from the fish and 40° above it. If the fish located the prey, it swam directly towards it and consumed it. Any other reaction by the fish was classified as non-location.

Four vertical planes, 0°, 45°, 90°, and 135°, were considered to represent the total reactive volume. For measurement at 0°, the door of the enclosure was aligned so that the fish was parallel to the grid. Prey were then introduced into the tank along a 5-cm-wide area stretching in front of the fish, with boundaries defined by two cords strung tightly across the top of the aquarium. Only prey within this band were considered to be at 0°. To investigate fish reaction to prey at 45°, the enclosure was rotated so that the door pointed at a 45° angle to the band where prey were introduced. The enclosure was rotated another 45° to obtain measurements on the reactive volume at 90°, and 45° further for measurements at 135°.

After each observation within the plane of interest, the fish was given four or five prey placed at random within the aquarium; this procedure assured that the fish would continue to search the entire water volume. The enclosure could also be raised and lowered to allow a range of vertical distances (0° to ± 90°) to be investigated within each plane. Thus the site of each prey presented within each vertical plane was recorded as centimetres away from the fish and degrees above or below it, with 0° representing the horizontal plane defined by the fish.

The aquarium was illuminated with two 150-W floodlamps suspended overhead. The light intensity was 5900 lx at the surface and 3500 lx at the bottom of the tank; since both are well above the light threshold of sunfish (Vinyard and O'Brien 1976), any differences in visual acuity from the top of the tank to the bottom was minimized. Grey-green posterboard provided background coloration.

To measure the location volume in the 0° horizontal plane, we used a large shallow Plexiglas tank 1.22 × 1.83 × 0.15 m and placed a set of polar coordinates on its bottom. Within the tank was a triangular enclosure similar to the wedge-shaped one described previously. As before, fish were trained to enter the enclosure, turn around, and search for prey once the enclosure door was opened. The site of the prey and the fish's response were defined as described above. Lighting was provided by room fluorescent lights at 260 lx. Grey-green posterboard provided background coloration.

Approximately 300 trials were run to measure location volume in each of the four vertical planes and in the 0° horizontal plane. A scattergram of the coordinates for both located and non-located prey was plotted for each plane. To define the area within which fish could locate almost all prey (≥95%), we averaged the closest two distances at which prey were not located in each plane, then connected these points with a smooth curve. Similarly, we averaged the farthest two distances at which the fish did locate prey in each plane to define the area outside of which almost no prey (≤5%) can be located.

Because experiments in the two tanks were performed under different light intensities, the distances at which fish could locate prey in the 0° horizontal plane under 260 lx were slightly lower than those recorded during the vertical plane studies under an average light intensity of 4700 lx. Thus we devised a normalization factor by comparing the 95% and 5% location distances for 2-mm prey within the overlapping regions of the two conditions, and found that a 1.27 increase in the measurements made under the lower light intensity provides the best average correction.

We also measured location volume under two lowered light intensities that are more typical of natural situations: 36 lx and 0.91 lx. For these measurements, a space large enough for the fish tank used in determining the location in the vertical planes and two observers was entirely enclosed in black plastic, and a rheostat was used to reduce the available light. Because of the light extinction from the surface to the bottom of the tank, measurements were restricted to a narrow arc in the center of the forward-directed vertical plane. Otherwise, the procedures for determining location volume were identical with those described above, with the exception that a high-contrast grid was used under the lowest light intensity.

Results and Discussion

Location Volume at High Light Intensities

When light intensities were high, bluegills were able to locate 2-mm *Daphnia* prey within 20 cm with almost certainty in all planes. As the distance between the fish and prey increased, the probability of the fish locating the prey decreased, with the maximum distance at which fish could locate prey varying with the angle of presentation (Fig. 1–5).

Forward-directed vertical plane — Figure 1 shows the sites of all prey presented in the forward-directed (0°) vertical plane, with the areas of 95% and 5% location probability defined. In this plane bluegills have the highest probability of locating prey if they are placed directly in front of it (at 0° horizontally within the 0° vertical plane). Fish located prey as far as 52 cm away when they were along the 0° horizontal line, but failed to see prey placed quite close but directly above (+90°) or below (−90°) them. This can be explained by the morpology of the fish's head, which causes two small blind spots in its visual field.

A *G*-test (Sokal and Rohlf 1969) showed large differences in the bluegill's ability to locate prey placed at different angles

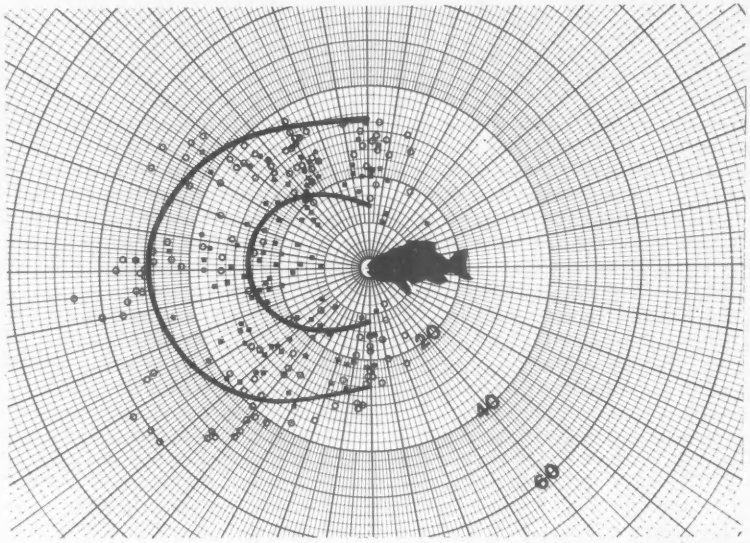

FIG. 1. Location of 2-mm *Daphnia magna* in the forward-directed vertical plane at about 5900 lx. The solid squares represent points at which prey were located while the open circles represent points where prey were placed but not located. The line closest to the fish bounds the region where location is almost certain (95%) while the outer line demarks the region past which prey are rarely located (less than 5% of the time). In the region between the two lines, the likelihood of location gradually increases as prey are placed closer to the inner line. Numbers refer to distance from the bluegill (cm).

in the forward-directed vertical plane ($G = 11.7$; $P < 0.01$), and at different distances from the fish ($G = 23.0$; $P < 0.005$). Such results clearly show that the ability of fish to detect prey varies with both angle and distance. Interestingly, the 95% location contour line at 0° horizontally, or the point directly ahead of the fish where it sees almost all prey, falls very close to the reported reactive distance of bluegill sunfish to similar sized prey at high light intensities (Werner and Hall 1974; Confer and Blades 1975; Vinyard and O'Brien 1976) (see Fig. 6). It thus appears that reactive distance may be a measure of the distance at which a fish recognizes a prey as edible, rather than a measure of absolute location ability. We found bluegills to locate prey at distances considerably greater than reactive distance measurements would suggest. In these cases, fish already moving toward distant prey would often "react" (pause briefly, then accelerate rapidly toward the prey). Thus reactive distance measurements underestimate ability of fish to locate possible prey. For this reason, we refer to the volume a fish searches as its location volume rather than its reactive volume.

The 45° vertical plane — As in the forward-directed plane, when prey were placed at a 45° angle, the fish were most likely to locate prey and could see them at the greatest distances when they were placed near the 0° horizontal line (Fig. 2). The poorest area of prey location was directly above (+90°) and directly below (−90°) the bluegill's head. The *G*-test for independence again showed large differences in the bluegill's ability to locate prey placed at different angles in the plane ($G = 31.43$; $P < 0.005$), and at different distances from the fish ($G = 237.32$; $P < 0.005$.

It is interesting that bluegills can locate prey at greater distances in this plane of the visual field than in the forward-directed plane (compare Fig. 1 and 2) even though bluegills have a small area of binocular vision directly ahead of them. Holling (1966), working with mantids (*Heirocula crassa*), a predator with a large area of binocular vision, found that the area of greatest prey recognition was directly in front of the predator. However, it is known that some fish are nearsighted when looking directly forward (Hoar and Randall 1971). It may be that bluegills make a small sacrifice in forward-directed location ability in exchange for nearsighted vision that assures accuracy in attacking prey that are close to the mouth.

The 90° vertical plane — Once again in the 90° vertical plane the fish located prey with the least difficulty along the 0° horizontal line (Fig. 3). Prey placed above or below this were located only when close to the fish. The *G*-test for independence showed large differences in the bluegill's ability to locate prey placed at different angles in the plane ($G = 37.9$; $P < 0.005$) and at different distances from the fish ($G = 13.2$; $P < 0.05$). The blind spots again were evident, and the absolute magnitude of the prey location distances was slightly less than for the more forward-directed planes.

In a study of lake trout, Confer et al. (1978) reported blind spots directly above and below the fish, but found fish to

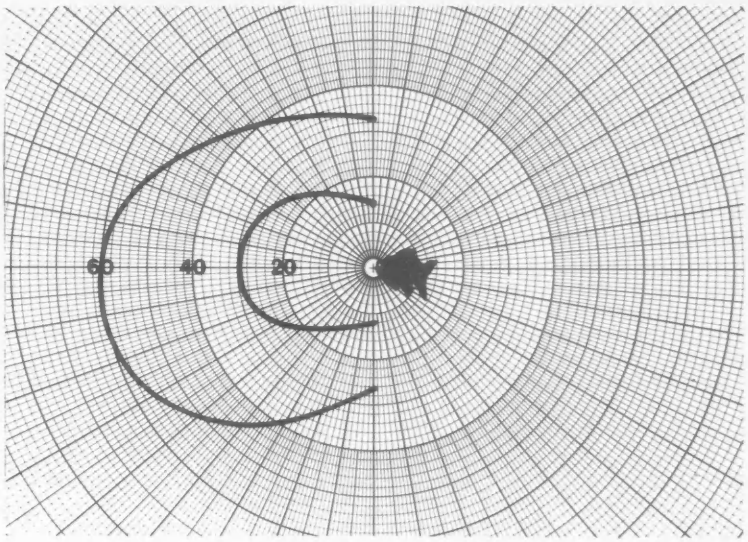

FIG. 2. Location of 2-mm *Daphnia magna* in the vertical plane 45° off forward directed at 5900 lx. Numbers refer to distance from the bluegill (cm).

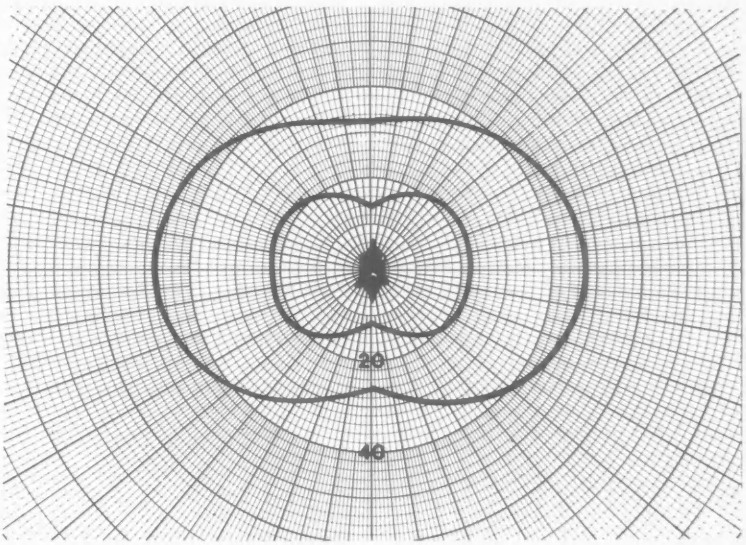

FIG. 3. Location of 2-mm *Daphnia magna* in the vertical plane 90° off forward directed at 5900 lx. Numbers refer to distance from the bluegill (cm).

locate prey placed to the side at the same distances as they located prey in front of them. Lake trout and planktonic salmonids, because they commonly feed in the pelagia of oligotrophic lakes where prey are scarce, may have to search a greater volume to locate adequate food than do bluegills that generally feed in or near the littoral (Werner et al. 1977) of productive lakes. Thus, the location volume of salmonids may be shaped differently than that of bluegills.

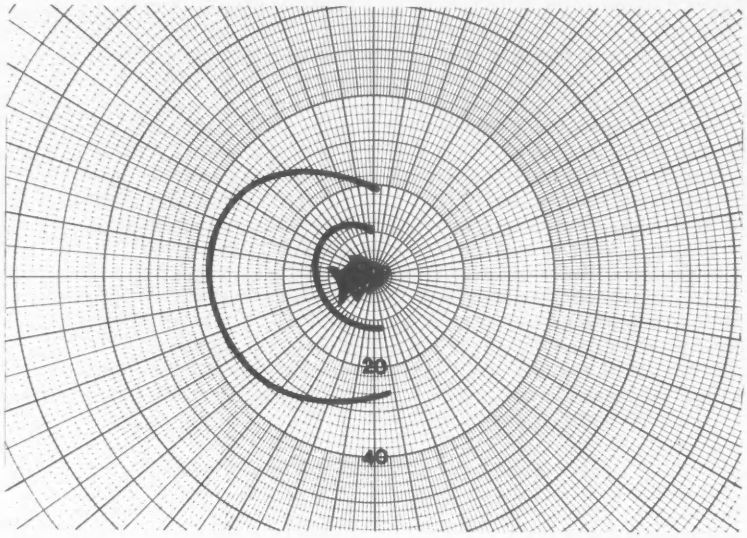

FIG. 4. Location of 2-mm *Daphnia magna* in the vertical plane 135° off forward directed at 5900 lx. Numbers refer to distance from the bluegill (cm).

The 135° vertical plane — Bluegills had considerable difficulty locating prey in this plane (Fig. 4). The *G*-test again demonstrated that the probability of the fish locating prey varied with distance ($G = 34.29$; $P < 0.005$), but in this plane the angle at which prey were presented made no difference ($G = 1.86$; $P < 0.05$) because prey location probabilities were so low at all angles.

The 0° horizontal plane — When prey were presented at 0° horizontally to the fish, we found that bluegills were able to locate prey at the greatest distances 45° to the side (Fig. 5), corroborating the measurements in the vertical planes. Fish were least able to see prey placed slightly behind them (135°). The *G*-test for independence showed large differences in the bluegill's ability to locate prey among different angles in the plane ($G = 11.7$; $P < 0.01$) and between prey located different distances from the fish ($G = 23.0$; $P < 0.005$).

In general, the 95% and 5% location probability contours in the 0° horizontal plane (Fig. 5) appear quite similar to those described for the four vertical planes (Fig. 1–4). The increased ability of fish to locate prey at a 45% angle is most obvious in the 0° horizontal representation. Also evident is the decrease in location ability to the sides (90°) and behind (135°) the fish, making the 95% location distance at a 45° angle almost twice that at a 135° angle.

Confer et al. (1978) reported that lake trout were able to locate prey at the greatest distances when prey were placed slightly behind the fish (corresponding to our 135° vertical plane). The considerable differences in the methods used in their experiments as compared to those in the present study may account for the different results obtained, or it may be that centrarchids and salmonids differ in this regard.

Confer (personal communication) suggests that some of the difference between the two studies (the present one and Confer et al. 1978) may be due more to differences in methodology than in species of fish. He suggested that a swimming fish may not search the entire volume as efficiently or thoroughly as an initially stationary fish such as used in the present study. This would account for the fact that Confer et al. (1978) found that their measured distances were significantly shorter than previously published forward-directed reactive distances for similar prey under identical light conditions. In the present study, of course, we find location distance to be generally greater than forward-directed reactive distances. These differences may occur in the field as a result of differences in movement patterns, since bluegills commonly hesitate slightly after consuming one zooplankton prey before pursuing the next, whereas some salmonids may come closer to cruising constantly.

REACTIVE VOLUME AT LOWERED LIGHT INTENSITIES

To extrapolate the location volume results to more natural conditions, we investigated the distances at which bluegills located prey under low light conditions. At 35 lx, which is a more typical light intensity in lakes at midday, the ability of the fish to locate prey is reduced by about 25%. At 0.91 lx, representing lakes at dusk and dawn, the reduction in the ability of fish to locate prey is as much as two-thirds (Fig. 6). When these results are compared to measured reactive distances of bluegills to 2-mm *Daphnia* under similar light conditions, the line of 95% probability is similar to reactive distance reports (Vinyard and O'Brien 1976) (Fig. 6). This further indicates that reactive distance measurements are underestimates of ability of fish to locate prey and probably

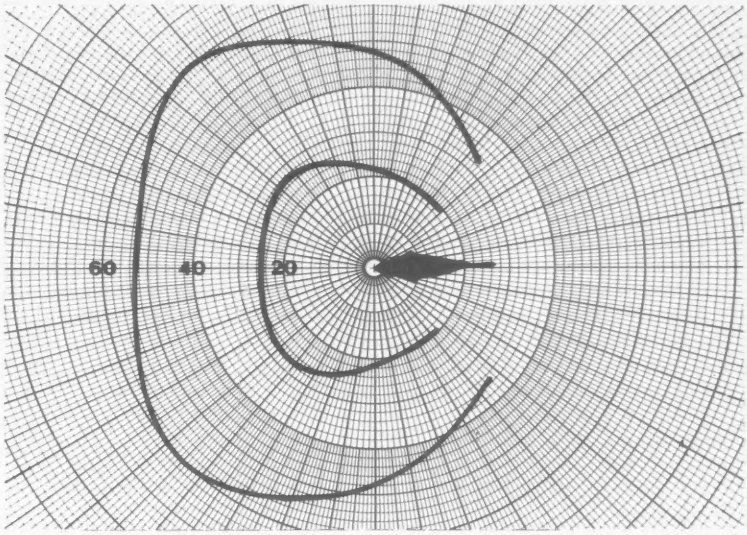

FIG. 5. Location of 2-mm *Daphnia magna* in the horizontal plane surrounding the fish corrected to light intensities equivalent to 5900 lx. Numbers refer to distance from the bluegill (cm).

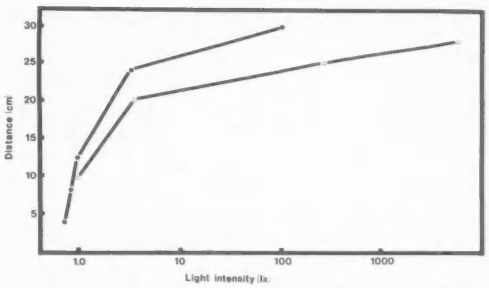

FIG. 6. Comparison of the reactive distance (Vinyard and O'Brien 1976) to the 95% prey location contours at varying light intensities. Solid circles represent reactive distance; open circles represent the 95% prey location contours for prey placed directly in front of the fish.

represent the point at which a fish clearly recognizes prey as potential food, and not the distance at which it can first see an object. However, because the location volume is closely correlated with the reactive distance, earlier reports of reactive distance at a variety of light and turbidity conditions (Vinyard and O'Brien 1976) can be used to generate location volume contours for bluegills under a wide range of situations.

General Discussion

Past models of fish predation of zooplankton have been based on assumptions that the volume searched was a sphere, hemisphere, or cylinder with radius equal to the forward-directed reactive distance (Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976; Eggars 1977). In this study, we found that the fish have a considerable likelihood of locating prey well beyond the measured reactive distance, which actually represents the zone within which prey are almost certain to be seen. Our second finding, that bluegill see prey at greatest distances when they are placed at a 45° angle rather than straight ahead, further indicates that earlier models may considerably underestimate the volume searched by fish.

The uneven ability of bluegills to locate prey in various areas of the location volume (Fig. 1–5) may indicate non-uniform distribution and density of visual receptors in the bluegill's eye. Receptors may be more dense in retinal areas corresponding to 0° and 45° than in those corresponding to 90° and 135°. Alternatively, differential processing of visual input from different areas of the retina could also explain the uneven visual acuity.

Although most fish do not have a true fovea, many species have a macular area characterized by a high density of cones and a relative absence of blood vessels (Prince 1956; Hoar and Randall 1971). In a study of several species of marine teleosts, O'Connell (1963) described a macular area in four species of clupeids. The areas were found ventral-temporally in the retina, corresponding to the forward-directed and surface-feeding habits of the fish. Verheigen (1969) reported the presence of a ventral fovea in another surface-feeding clupeid.

The shape of the bluegill's retina may be responsible for the fish's decreased ability to locate prey directly in front of them. Pumphrey (1961) found the trout retina to be somewhat ellipsoidal, and suggested that the greater distance between the lens and the back of the retina caused the trout to be

myopic when looking at objects directly in front of it. Myopia may be an advantage under low light intensities and in assuring capture of evasive prey.

The description of the location volume of bluegills reported here shows clearly that bluegills are much better able to see prey within the forward hemisphere. However, it is also evident that there are no absolute limits to search, but rather that the probability of a fish detecting prey declines continuously with distance. Measures of reactive distance alone are not adequate descriptors of fish prey location ability; thus, existing models of fish feedings should be modified to include the larger volume that is actually searched by the fish.

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CONFER, J. L., AND P. I. BLADES. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571–579.

CONFER, J. L., G. L. HOWICK, M. H. CORZETTE, S. L. KRAMER, S. FITZGIBBON, AND R. LANDESBERG. 1978. Visual predation by planktivores. Oikos 31: 27–28.

EGGARS, D. M. 1977. The nature of prey selection by planktivorous fish. Ecology 58: 46–59.

HOLLING, C. S. 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 41: 385–398.

1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48: 1–86.

HOAR, W. S., AND D. J. RANDALL. 1971. Fish physiology. Vol. V. Academic Press, New York, NY.

O'BRIEN, W. J. 1979. The predator–prey interaction of planktivorous fish and zooplankton. Am. Sci. 67: 572–581.

O'BRIEN, W. J., D. KETTLE, AND H. RIESSEN. 1979. Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. Ecology 60: 287–294.

O'BRIEN, W. J., N. A. SLADE, AND G. L. VINYARD. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042–1052.

O'CONNELL, C. P. 1963. The structure of the eye of *Sardinops caerula*, *Engraulis mordux*, and four other pelagic marine teleosts. J. Morphol. 113: 287–329.

PRINCE, F. H. 1956. Comparative anatomy of the eye. Charles C. Thomas, Publisher, Springfield, IL.

PUMPHREY, R. J. 1961. Concerning vision, p. 193–208. *In* J. A. Ramsey and V. B. Wigglesworth [ed.] The cell and the organism. Cambridge University Press, London.

SCHMIDT, D., AND W. J. O'BRIEN. 1981. Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. (In press)

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

VERHEIGEN, F. J. 1969. A peculiar nystagmus and a corresponding foveal structure in the eye of the herring (*Clupea harengus* L.). Experientia 15: 443–447.

VINYARD, G. L., AND W. J. O'BRIEN. 1976. Effects of light and turbidity on the reactive distance of bluegill sunfish (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33: 2845–2849.

WARE, D. M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 787–797.

WERNER, E. E., AND D. J. HALL. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042–1052.

WERNER, E. E., D. J. HALL, D. R. LAUGHLIN, D. J. WAGNER, L. A. WILSMANN, AND F. C. FUNK. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34: 360–370.

ZARET, T. M. 1972. Predators, invisible prey, and the nature of polymorphism in the Cladocera (Class Crustacea). Limnol. Oceanogr. 17: 171–184.

ZARET, T. M., AND W. C. KERFOOT. 1975. Fish predation on *Bosmina longirostris*: Body size selection versus visibility selection. Ecology 56: 232–237.

ZARET, T. M., AND J. S. SUFFERN. 1976. Vertical migration in zooplankton as a predation avoidance mechanism. Limnol. Oceanogr. 21: 804–813.

Interspecific Associations in a Woodland Stream

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REICE, S. B. 1981. Interspecific associations in a woodland stream. Can. J. Fish. Aquat. Sci. 38: 1271–1280.

Patterns of association of benthic macroinvertebrates were examined within a riffle of New Hope Creek, North Carolina, USA. The 16 most common species were tested for cooccurrences. Chi-square contingency tests on simultaneous presence and absence of two species at a time were performed. The strength of the association and its direction were determined for significantly associated species pairs using the *V* statistic. The patterns of association among 120 species pairs are presented for each of three mineral substrate types (cobbles, pebbles, and gravel) and leaf packs (5 g of *Cornus florida* leaves) attached to them. These data were collected over a 3-mo period.

The results show that significant interspecific association on a given substrate was found for 18.3% or less of the species pairs. The species which strongly associated on one substrate type differed from those associating on another substrate. The presence or absence of leaf packs on a mineral substrate patch, which did not affect most species densities, did affect the cooccurrence patterns among species. The presence of leaf packs reduced the number of significantly associated species pairs on all substrates. In all cases in mineral substrates, negative associations were rare. The proportion of negative associations approximated what one would predict by chance alone. This suggests that competition may not be an important factor in stream communities.

This work presents a different approach to the analysis of lotic communities. It suggests several hypotheses about community structure in streams. It reaffirms that substratum type is a major governing factor in stream community structure and dynamics.

Key words: benthic macroinvertebrates, community organization, competition, interspecific association, leaf pack, patchiness, predation, stream, substrate

REICE, S. B. 1981. Interspecific associations in a woodland stream. Can. J. Fish. Aquat. Sci. 38: 1271–1280.

Nous avons étudié les caractéristiques des associations de macroinvertébrés benthiques dans un maigre du ruisseau New Hope, en Caroline du Nord (É.-U.). Sur les 16 espèces les plus communes, nous avons vérifié la fréquence des co-occurrences. Des tests de contingence par khi carrés de la présence et de l'absence simultanées de deux espèces à la fois ont été effectués. La statistique *V* a servi à déterminer la cohésion et la direction de l'association de paires d'espèces à co-occurrence significative. Nous décrivons les caractéristiques d'association de 120 paires d'espèces avec chacun de trois types de substrats minéraux (galets, cailloux et gravier), et avec paquets de feuilles (5 g de feuilles de *Cornus florida*) qui y sont attachés. Nous avons recueilli ces données sur une période de 3 mois.

Une association interspécifique significative sur un substrat donné a été observée chez au moins 18,3 % des paires d'espèces. Les espèces étroitement associées à un type de substrat diffèrent de celles associées à un autre substrat. La présence ou l'absence de paquets de feuilles sur une parcelle de substrat minéral, sans influence sur la densité de la plupart des espèces, influent sur la co-occurrence des espèces. La présence de paquets de feuilles réduit le nombre de paires associées sur tous les substrats. Dans tous les cas, sur les substrats minéraux, les associations négatives sont rares. La proportion de ces dernières est à peu près la même que celle prédite par chance seulement. La concurrence ne serait donc pas un facteur important chez les communautés des cours d'eau.

L'étude décrite ci-dessous est une approche différente de l'analyse des communautés lotiques. On y avance plusieurs hypothèses sur la structure des communautés fluviatiles. On

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y démontre de nouveau que le type de substrat joue un rôle majeur dans la structure et la dynamique de ces communautés.

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SUBSTRATUM particle size has been identified as a major determinant of the distribution and abundance of lotic macroinvertebrates; Cummins and Lauff (1969), Allan (1975), Higler (1975), Minshall and Minshall (1977), Rabeni and Minshall (1977), Hart (1978), Wise and Molles (1979), Shelly (1979), and Reice (1980) have analyzed the role of substratum in detail. Current velocity is positively correlated with substratum particle size (Moon 1939), and many workers have sought to partition their relative effects (Linduska 1942; Scott 1958; Ulfstrand 1968; Egglishaw 1969; Rabeni and Minshall 1977; Reice 1980). Several of the most recent studies have demonstrated that substratum size has a far greater effect than current velocity on animal distributions in streams. Minshall and Minshall (1977) showed that microdistribution patterns in a riffle were determined more by substratum size than velocity. Rabeni and Minshall (1977) showed that direct velocity effects were insignificant compared with substratum-related trapping of detritus particles. Peckarsky (1980) showed little response by total benthic invertebrates to detritus enrichment. Reice (1980) manipulated substratum particle size in a New Hope Creek, NC, USA riffle and showed that most common taxa selected different substrata even when velocity differences were minimized.

Although the effects of physical factors (substratum size and current velocity) have been well documented, relatively little attention has been given to the role of biotic interactions in streams. The investigations have been few and the results are somewhat contradictory. Peckarsky (1979, 1981) demonstrated intraspecific and interspecific responses to benthic density. This implicates competition as an important factor in lotic macroinvertebrate microdistributions. Allan's (1975) work suggests that competition is rarely important in faunal replacements. Peckarsky and Dodson (1980a, b) suggest that benthic invertebrate predators do not respond to prey density but that prey respond to their presence. Obendorfer et al. (1980) demonstrated prey selectivity by two predators and a response in decomposition rate of leaf packs. Allan (1975, 1978) suggests that fish predation has major effects on lotic benthic macroinvertebrate abundance. Whereas interspecific interactions are well understood in other aquatic systems (lakes, ponds, rocky intertidal zone, etc.), we have only a few bits of preliminary information from streams. In this paper, I will present data from an experiment that will help us understand the importance of interspecific interations in lotic benthic communities.

The presence and extent of interspecific interactions can be deduced from distributional data (Krebs 1978; Pielou 1977). I will present a matrix of pairwise associations of taxa that can be used as a measure of responses in manipulative experiments and will analyze the frequency, strength, and context of different patterns of interspecific associations. I will demonstrate that the web of interspecific associations in a single stream varies as a response to benthic substratum particle size and leaf pack presence or absence. These data will be used to develop the concept of community in a stream ecosystem.

Materials and Methods

SAMPLING DESIGN

In a study of microdistribution of benthic macroinvertebrates I sampled patches of replicate substratum of three sizes (cobbles, pebbles, and gravel) in a single riffle of New Hope Creek. This third-order stream is in a protected area of the Korstian Division of the Duke Forest, Orange County, NC, USA. The characteristics of the substrata are given in Table 1. Details of the measurements may be found in Reice (1980). The study was conducted in fall 1975 and winter 1976. Water temperature ranged between 8.8 and 2.3°C. Velocity did not vary significantly among patches. Means and standard errors for velocity on the three substrata were 17.2 ± 2.2 cm/s for cobbles, 18.4 ± 2.3 for pebbles, and 17.4 ± 2.6 for gravel. There was natural variation among sampling dates. Dissolved oxygen was above or near saturation on all dates.

Patches were constructed by filling an open-topped 25 × 25 × 10 cm basket of 6-mm-mesh hardware cloth with one of the three experimental substrates. Half of the baskets had three leaf packs each of *Cornus florida* (flowering dogwood) leaves attached (5 g each). All baskets were introduced on November 24, 1975. Baskets were randomly placed from bank to bank in the riffle. The riffle was 20 m long × 8 m wide and 25–50 cm deep. Less than 5% of the riffle had baskets on the surface. A set of samples was removed every 2 wk until January 26, 1976. A complete sample set was 18 baskets (3 substrata × 2 leaf treatments (with and without leaf packs) × 3 replicates) and 27 leaf packs. Six full sample sets were taken. Details of the sampling and results of the single species microdistributions can be found in Reice (1980). The overall objective of the experiment was to test the effects of leaf litter and substratum type on colonization and development of stream benthic communities, while minimizing the effects of current velocity.

Cooccurrence matrices for all common species pairs were generated for leaf pack and substratum samples separately. Because all leaf packs were virtually contiguous on a basket, they were treated as one common site. For example, if *Ephemerella doris* was found in leaf pack A and *Acroneuria abnormis* was in leaf pack B from cobbles basket 1 on a given date, they were treated as if they had cooccurred in the sample.

COOCCURRENCE MATRICES: GENERATION AND ANALYSIS

The analysis of patterns of distribution followed Pielou (1977). Each sample was examined for the presence or absence of each species. Then, for each species pair, each sample was classified according to the grid of Fig. 1. Therefore, "*a*" represents the number of samples in which species A and B cooccurred. Only presence–absence data were used and abundances were ignored. The extreme patchiness of distribu-

TABLE 1. Substrate characteristics.

	Longest axis ($\bar{x}\pm$SE, cm)	Shortest axis ($\bar{x}\pm$SE, cm)	Mean no. of particles per basket	Mean surface area per basket (cm^2)
Cobbles	12.08±0.34	4.72±0.21	12.4	4285
Pebbles	4.00±0.07	1.58±0.04	411.3	10858
Gravel	1.60±0.04	0.58±0.02	10989.3	42858

tion of the macrobenthic organisms makes parametric (conventional) correlation coefficients produce spuriously significant interactions. These are based on occasional co-occurrences with both species in abundance. The distribution of samples in the grid was tested by the chi-square 2 × 2 contingency test for deviation from randomness (Siegel 1956).

$$(1)\quad \text{chi-square} = \frac{N(ad - bc)^2}{mnrs}$$

This is appropriate for species which occupy discrete habitat units. This test, as Pielou (1977) points out, is quite crude. A significant chi-square contingency test shows a relationship without indicating whether the relationship is positive (a greater than expected, see Fig. 1) or negative (b and c greater than expected). It gives no clue as to the strength of the relationship. It actually tests whether the two species occur independently in the samples. More interesting and ecologically relevant is the strength and nature of the relationship. To determine this I calculated a second statistic, V.

$$(2)\quad V = \frac{ad - bc}{+(mnrs)^{\frac{1}{2}}}$$

V assumes values from +1 for complete positive association ($b = 0$, $c = 0$) to −1 for complete negative association ($a = 0$, $d = 0$). It equals zero when there is no association.

A note of caution is needed here. Simple analysis of distributional data, even in an association analysis, cannot give a definitive answer to the question "Are two species in competition?" If species are negatively associated, one could conclude that one species has competitively displaced the other. This conclusion is open to various alternative explanations, including (1) the species do not interact, (2) the species are keying in on different environmental features, and (3) the species have different physiological requirements. On the other hand, if species are positively associated, it may be that they are (1) mutually attracted to some site-specific exogenous variable, (2) positively interacting through some form of mutualism, or (3) negatively interacting as in predator–prey or competitive relationships. Further, any conclusion about competition must assume that some resource (or access to it) is limiting in nature. Competition which only limits population size will not be detected by this technique. Ultimately, the analysis of distributions must yield to manipulative experiments designed to determine explicitly the nature of the interspecific relationship. Given this cautionary warning, it is still profitable to examine distributional data for preliminary indications of the frequency and nature of interspecific interactions in the stream macrobenthic community.

	SPECIES B PRESENT	SPECIES B ABSENT	
SPECIES A PRESENT	a	b	m=a+b
SPECIES A ABSENT	c	d	n=c+d
	r=a+c	s=b+d	N=a+b+c+d

FIG. 1. 2 × 2 table of species cooccurrence to calculate chi-square and V statistics.

The data are presented in the form of matrices of V values, presenting values only for species pairs which show significant cooccurrence by the chi-square analysis ($P(\chi^2) \leq 0.05$, df = 1). Only the 16 most common taxa are considered. Chironomidae, which were pooled in the orginal analysis, will not be shown.

Patterns of cooccurrence are analyzed considering the known substratum preferences (Reice 1980) and functional groups (Cummins and Klug 1979), as given in Merritt and Cummins (1978), of the fauna. This will help me to distinguish between potentially real and spurious interactions.

Results and Discussion

Analysis of single species microdistributions can be found in Reice (1980). In general, most taxa (9 of 16) preferred either leaf packs or the underlying substrata. Consequently, the cooccurrence matrices for mineral and leafy substrata are analyzed separately. Because most taxa specialized on particular mineral substrata (10 of 16 showed preference for one or more sizes), cooccurrences on cobbles, pebbles, and gravel are treated separately. The object is to analyze cooccurrence and species interactions in biologically meaningful habitat units. Table 2 summarizes the number, mean, and standard deviation (absolute value) for significant V values for various subsets of the data.

SUBSTRATUM-SPECIFIC ASSOCIATIONS

Figures 2, 3, and 4 present the V values for significantly associated pairs of taxa on gravel, pebbles, and cobbles, respectively. When all substrata are pooled, the highest number of species pairs display a significant degree of cooccurrences, with 36 of 120 or 30% of all pairs cooccurring. However, the strength of association is relatively weak ($\bar{x}_v = 0.299$). It is helpful to think of V as a nonparametric correlation coefficient. Note that on gravel there are fewer significant associations, but they have greater overall strength ($n = 21$ or 17.5%, but $\bar{x}_v = 0.652$). This pattern holds on pebble and

TABLE 2. Frequency, strength, and sign of association by microhabitat.

	n^a	+	−	$\bar{x}^b$	SE^b
All substrata pooled	36	36	0	0.299	0.075
All gravel substrates	21	21	0	0.652	0.190
With leaf packs	5	5	0	0.648	0.071
Without leaf packs	17	17	0	0.807	0.176
All pebble substrates	22	21	1	0.560	0.145
With leaf packs	3	3	0	0.595	0.094
Without leaf packs	22	21	1	0.703	0.166
All cobble substrates	8	5	3	0.410	0.040
With leaf packs	5	4	1	0.613	0.052
Without leaf packs	7	4	3	0.573	0.057
All leaf packs	11	6	5	0.356	0.073
Leaf packs on gravel	7	6	1	0.715	0.180
Leaf packs on pebbles	2	0	2	0.556	0.030
Leaf packs on cobbles	7	6	1	0.599	0.060

[a]Number of species pairs with $P(\chi^2) \leq 0.05$, theoretical maximum = 120.

[b]Absolute value of V ($\bar{x} \pm$ SE).

cobble substrates also. The inflation of the number of significant associations on all substrata pooled derives from the different sets of taxa associated on different substrata. This is analogous to having a strong main effect causing a significant but weak two-way interaction in an analysis of variance. Of the 21 significantly associated pairs on gravel (Fig. 2) and 22 on pebbles (Fig. 3), only 5 are significant on both substrata. The set of associations on cobbles (Fig. 4) overlaps by 1 pair with the set on pebbles and none with the set on gravel. The majority of species pairs are associated only on a particular substrate type. This indicates that there are indeed significant substrate-specific associations in streams (Reice 1974, 1977).

A similar pattern is present in leaf packs on various substrata. There are more cooccurrences on all leaf packs pooled (Table 2), and the mean V value is lower than on any single substratum. Each substratum type harbors a nearly unique set of cooccurring taxa in leaf packs on its surface. This is in spite of the fact that only 2 of 16 species showed significant variation in their distribution in leaf packs due to the underlying substrate type (Reice 1980). *Allocapnia* prefers leaf packs on cobbles and pebbles, and *E. doris* selects leaf packs on pebbles. One would anticipate no significant pattern of cooccurrences on a substrate-specific basis but it is there nonetheless.

Another new pattern revealed by association analysis is the effect of the presence of leaf packs on the interactions between species in the substrata. Of the 16 taxa analyzed singly, only one differentiates between substrata with or without leaf packs on the surface. *Allocapnia* (Plecoptera) prefers substrata with leaf packs (Reice 1980). This species is a shredder, i.e. a species which feeds on leaves and other coarse particulate organic matter (CPOM) and produces fine particles. It normally is found in leaves and in this study it displays a strong preference for leaf packs over substrata. My earlier conclusion (Reice 1980) was that "the presence of a leaf covering is generally an insignificant factor in the choice of a patch by lotic invertebrates."

The comparison by association analysis of individual substrate types with and without leaf packs gives a totally different perspective (Table 2, Fig. 5 and 6). In all three substrate types, there are many more cooccurring pairs when leaf packs are absent than when they are present. In gravel without leaf packs there are 17 significantly cooccurring pairs whereas in gravel with leaf packs there are only 5; in pebbles there are 22 pairs without leaf packs and only 3 with leaf packs; in cobbles the decline is only from 7 to 5. Furthermore, the cooccurring species pairs in substrata with leaf packs present are often different from the ones that cooccur when leaf packs are absent. In cobbles no pair showing significant association under one condition did so in the other. In pebbles two of the three pairs which are associated with leaf packs present are also associated when leaf packs were absent. In gravel only one of five cases overlap. These shifts in distribution open many interesting questions about the autecology and community dynamics of lotic macroinvertebrates. The responses of species pairs to the presence or absence of leaf packs is a new finding provided by the analysis of cooccurrence matrices. It demonstrates that the degree of association of species with each other is at least as sensitive a parameter as the individual species' distributions.

The reason(s) for these differences is (are) unclear. The leaf packs on the surface of the sample basket account for approximately half of the the upper surface of the basket. This leafy covering partially restricts access by predators such as fish that feed from above. If the leaf packs reduced predation pressure, then species in these covered baskets might have increased interactions with each other. If such predation is more frequent or intense in the leaf pack free baskets, competitive interactions would be less likely to result in competitive exclusion and coexistence would be enhanced. This hypothesis, although attractive, is unsupported by the data. If it were correct, we should expect higher V values with leaf packs present. In cobbles the mean absolute V value (Table 2) is about the same with and without leaf packs. In pebbles and gravel the mean absolute V value is actually somewhat higher without leaf packs. This means the strength of association is the same or reduced with leaf packs partially blocking access from the top. Further, where negative associations occur, all four cases (three on cobbles, one on pebbles) occur without leaf packs present. If anything, then, competitive interactions may be more common without leaf packs. However, the feeding of fish or other surface predators may concentrate on invertebrate predators. If that is the case then patches without leaf packs may actually have reduced total predation pressure. That may be why there are more interactions when leaf packs are absent. More study on predators' diets in streams will help to explain these results.

Another likely explanation is that the leafy cover substantially alters some physical or chemical parameter. If, say, dissolved oxygen is reduced or velocity increased, the environmental conditions necessary for continued survival in the microhabitat may be altered for all species. If the range of conditions is effectively narrowed then the zone of acceptable environmental parameters would be restricted, limiting the shared niche space for interacting species. This would limit the number of significantly cooccurring pairs. The microhabitat requirements for coexistence or cohabitation in

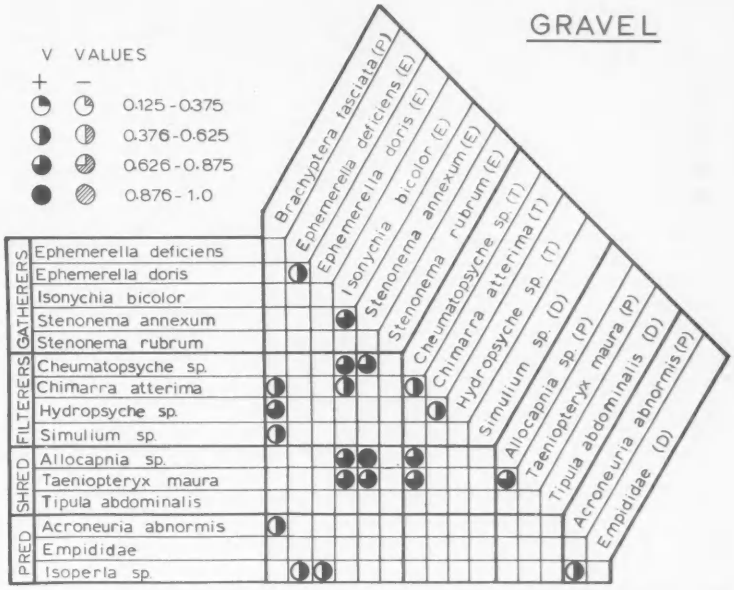

FIG. 2. Species association matrix showing ranges of *V* (strength of association) for signficiantly co-occurring pairs (see text) in gravel substrata. P, Plecoptera; E, Ephemeroptera; T, Tricoptera; D, Diptera.

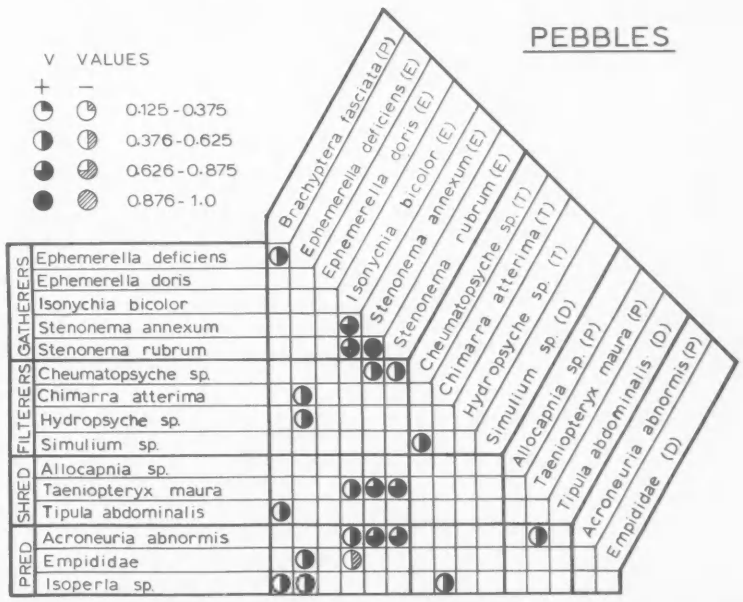

FIG. 3. Species association matrix showing ranges of *V* for significantly cooccurring pairs in pebbles. P, Plecoptera; E, Ephemeroptera; T, Tricoptera; D, Diptera.

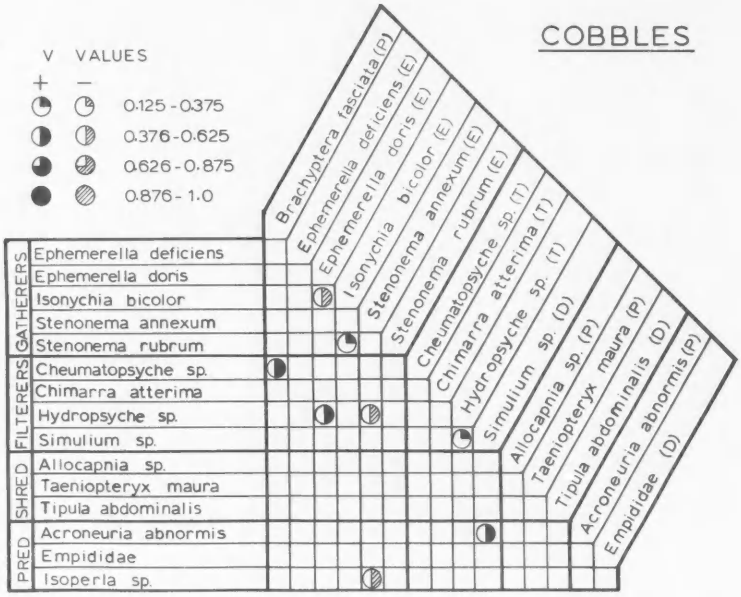

FIG. 4. Species association matrix showing ranges of *V* for significantly cooccurring pairs in cobbles. P, Plecoptera; E, Ephemeroptera; T, Tricoptera; D, Diptera.

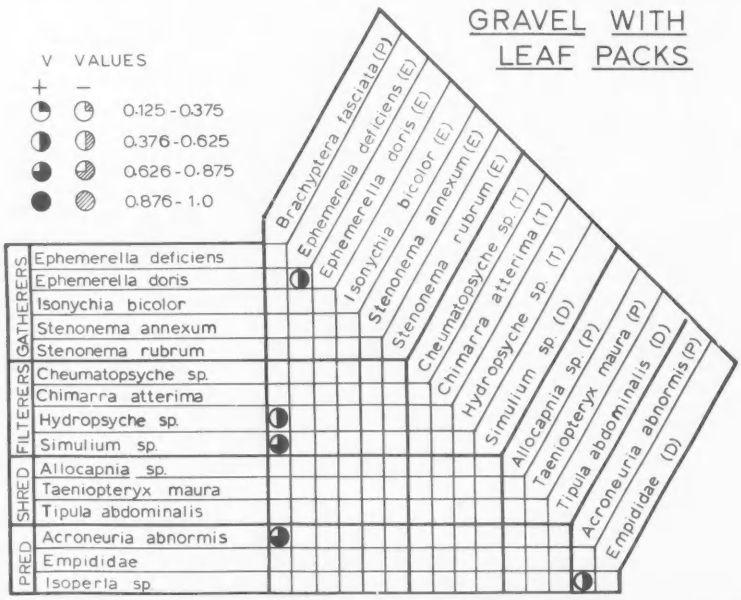

FIG. 5. Species association matrix showing ranges of *V* for significantly cooccurring pairs in patches of gravel with leaf packs covering the surface. P, Plecoptera; E, Ephemeroptera; T, Tricoptera; D, Diptera.

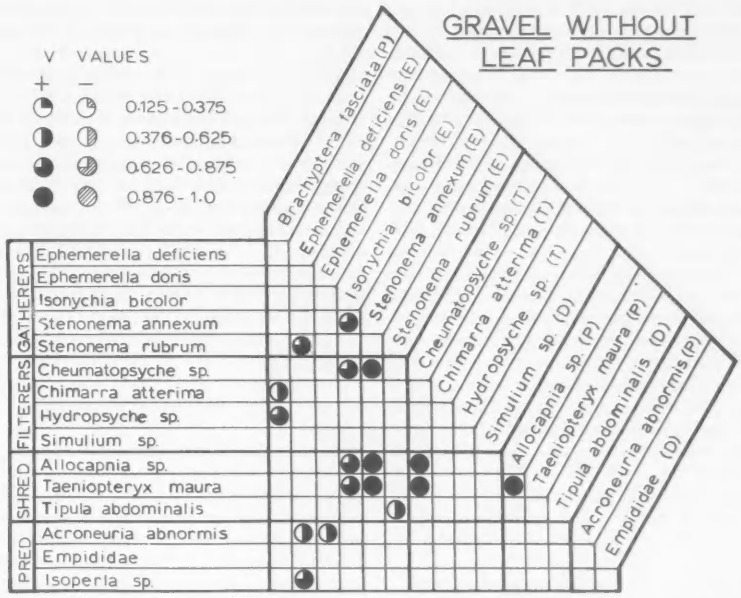

FIG. 6. Species association matrix showing ranges of *V* for patches of gravel without a covering of leaf packs. P, Plecoptera; E, Ephemeroptera; T, Tricoptera; D, Diptera.

environmental patches are likely to be more stringent than for single species presence or absence. Any alteration of the habitat would select more heavily against species pairs than against each species individually.

Evidence for Competition in Stream Benthos

One can begin to analyze the role of competition in stream communities by examining the frequency and nature of the negatively associated species pairs (Table 2). This presumes that strong disassociation is a likely result when interspecific competition is important. There are relatively few negative associations in mineral substrata. There are none in gravel (0 of 25), 1 of 25 significant associations on pebbles, and 5 of 13 in cobbles. These figures represent the total of unique, significant associations from each substratum (i.e. associations on all cobbles, cobbles with leaf packs and cobbles without leaf packs summed, etc). The proportions increase in leaf packs to one of seven negative associations in leaf packs on gravel and cobbles. Both of the associations in pebbles are significantly negative. Thus the combined fraction for substrata is 6 of 63 or 9.5% whereas in leaf packs it is 4 of 14 or 28.6%. Recall that we expect 1 of 40 or 2.5% to be negatively associated by chance alone (1 of 20 will have a significant association and half of those should be negative). With our knowledge of the substratum preferences of the species (Reice 1980) and their feeding groups (Merritt and Cummins 1978; Cummins and Klug 1979), we can examine which of these negative associations possibly reflect actual competitive exclusion.

In pebbles, the sole negative interaction is between *Isonychia bicolor*, a collector–gatherer, and a dance fly (Empididae). Dance flies are usually predators but are occasionally collector–gatherers. These species have contradictory microhabitat preferences. The fly was abundant in leaf packs and rare in mineral substrata, with 85% of all individuals found in leaf packs. *Isonychia bicolor* had 99% of all its individuals in mineral substrata. They simply occupied different microhabitats. The same applies to the negative association of *E. doris* and *I. bicolor* on cobbles. Both of these mayflies are collector–gatherers but *E. doris* is found in leaf packs, particularly on cobbles and pebbles, whereas *I. bicolor* is in the mineral substrata. This may possibly be the result of competition leading to habitat partitioning. *Tipula abdominalis*, a large, leaf-shredding cranefly larva, is most common in leaves on cobbles whereas *Simulium*, a filter-feeding dipteran, lives attached to large rocks, without leaf packs. This negative association probably does not reflect competition but simply individual taxa seeking out their distinct microhabitat niches, appropriate to their mode of feeding.

Stenonema annexum accounts for three negative associations. It is a collector–gatherer that prefers pebbles and cobbles to gravel and mineral substrata to leaves; it is negatively associated with *Isoperla* (a predator), *Hydropsyche* (a net-spinning caddisfly), and *Brachyptera fasciata*. Although *Hydropsyche* and *Isoperla* have similar substratum preferences to *S. annexum*, competition for food can be ruled out. *Hydropsyche* filters fine particles out of the water column and utilizes distinctly different resources than *S. annexum*. On cobbles, *Isoperla* was somewhat more common in leaves than

S. annexum, which accounts for much of the negative association. If these species are in fact interacting, it is a predator–prey relationship with *S. annexum* avoiding *Isoperla*. Only one case in cobbles is potentially explicable by competition, the negative association of *B. fasciata* and *S. annexum*. Both species have the same food habits (collector–gatherers) and similar microhabitat preferences, although *Brachyptera* was more common on gravel. Therefore, their negative association may be consistent with a competition hypothesis. Of the six cases of negative association for species pairs on mineral substrata, only one (possibly two) suggests competition.

In leaf packs, negative association was more common (28.7% of all cases). Yet, the explanations are somewhat simpler. In leaf packs on cobbles *Hydropsyche* is disassociated from *Allocapnia*. The former is a net-spinning caddisfly and uses the cobbles for hold-fast points. It would tend to avoid leaf packs altogether. *Allocapnia* is a shredder and prefers leaf packs. This is not competition, but microhabitat specialization. In leaf packs on pebbles, *Hydropsyche* and *Cheumatopsyche* are negatively associated. This may reflect competition as both are net-spinners. They are morphologically very similar taxa. However, neither is a normal resident of leaf packs. Their infrequent appearances did not coincide. In leaf packs on gravel, two collector–gatherers, the mayflies *E. doris* and *S. annexum*, show negative association. *Stenonema annexum* prefers mineral substrata and *E. doris* prefers leaves. This alternative preference may be the result of competition. Finally, *S. annexum* and *B. fasciata* are disassociated in leaf packs on pebbles. They are the same pair of probable competitors from the cobble substratum. So, two or three pairs of species stand as potential competitors in leaf packs.

Within either orders or functional groups, evidence for competition is very rare. Among congeners there are no negative associations. For mineral substrates only 2 of 63 or 3.2% of all significantly associated pairs are potentially due to competition. In leaf packs, possibly 3 of 14 or 21.4% are attributable to competition. Of the entire 120 possible pairs, the occurrence of pairs showing distributions suggestive of competition are only 1.7% in mineral substrata and 2.5% in leaf packs. This is within the range one should expect by chance alone.

The Nature of Positive Associations

The overwhelming majority of all associations was positive. These taxa represent species with overlapping substrate preferences or predator–prey pairs. On mineral substrata 22% of the significantly associated pairs were predators associated with potential prey organisms. In leaf packs 29% of the significant pairs were predator–prey associations. Note that the association of a small predator like *Isoperla* with larger prey species (i.e. *Ephemerella* spp.) may imply predation which only rarely occurs.

Mutual preference for substrata is a good predictor of positive interspecific associations. However, the essence of the chi-square test is to ask "Given a tendency to associate (say by species A and B both preferring pebbles), do they cooccur more often than one would predict by chance alone?" These data suggest that about half of those species with similar substratum preferences did positively associate (15 of 28 or 53.6%).

There is no direct way to implicate mutualism or facilitation from these data. Short and Maslin (1977) showed that the shredder *Pteronarcys californica* increased food availability to the filtering collectors *Hydropsyche* and *Simulium*. In this study, on gravel substrata, the shredder *Allocapnia* was positively associated with *Cheumatopsyche*, a filtering collector. *Tipula*, a shredder, was similarly coupled with *Cheumatopsyche* in leaf packs on cobbles. Although this is probably an important interaction in the energetics of the stream community, the relationships are probably diffuse. It would be reasonable for filterers to be located downstream of shredders, but not necessarily in the same 25 × 25 cm patch of substratum. The spatial scale of such interactions is worth investigating.

Interpretation of Data

This use of microdistributional data in cooccurrence matrices reveals several interesting patterns that are worth pursuing. First and foremost, these data show that there are unique substratum-specific associations of benthic macroinvertebrates in streams. Species cooccurrence patterns reveal a degree of interaction which is totally unpredictable from individual population distributions. This is a good example of an emergent property (Caswell et al. 1972). The phenomenon is observable only through analysis of mutual distributions, i.e. a community level measure of association. There are significant couplings of taxa on the three experimental particle sizes tested, with minimal overlap between the sets of associated species. Whether these species clusters represent true component communities (Root 1973), i.e. coevolved, strongly interacting subunits of the stream community, is an important research question which remains unanswered. Careful experimental manipulations will be required to establish the biological significance of the substratum-specific species groups.

The data also show that factors such as a leaf covering on substrate surfaces can have a major effect on the microdistribution of species pairs. The interactions between species are apparently even more responsive to the alteration of the microhabitat than are individual species distributions. Hildrew and Edington (1979) analyzed the coexistence of six species of hydropsychid caddisflies. They found them to be arranged according to temperature, velocity, and diet. In one case a pair of congeners coexisted without apparent ecological differences. Vannote and Sweeney (1980) show how different thermal optima allow congeneric species of mayflies to coexist while minimizing competition. How small changes in niche dimensions and environmental parameters affect species interactions is an open field for research in streams.

These data suggest many possibilities about the biotic organization of stream communities. Recall that the analysis of distributions as a means of inferring interaction is inherently limited. These ideas are offered as a stimulus to further research.

The lack of negative associations between functionally and morphologically similar species suggests that competition is

relatively unimportant as a determinant of microdistributions in New Hope Creek. How does this compare to other ecosystems? It is in sharp contrast with most of the prevailing theory of community ecology, which is based on the rocky intertidal model of community organization (Paine 1966; Dayton 1971; Connell 1975; Menge and Sutherland 1976). That model shows that species composition results from a dynamic tension between competition and predation. Competition tends to simplify the community by eliminating poorer competitors through competitive exclusion. This tendency is counterbalanced by predators, whose various feeding strategies mitigate the effects of competition by harvesting the more common, competitively dominant species. This simultaneously reduces those species' abundances and relieves the competitive pressure on the inferior competitors. Thus predation permits more species to coexist resulting in higher species richness and diversity.

Stream communities have high species richness too. The total number of benthic macroinvertebrate species identified in the New Hope Creek watershed now exceeds 150. Yet, these data suggest that competition can be relatively unimportant in streams, a conclusion supported by Allan (1975). Given the similarity of species microhabitats, feeding habits, and body sizes, one might expect competition to be common and important in streams. However, three major factors mitigate against competition resulting in exclusion of a species in streams. First, resources are probably never limiting to stream herbivores or detritivores. In detritus-based streams such as New Hope Creek, detritus inputs are staggered throughout the year so that detritus (food) is always abundant (S. R. Reice, University of North Carolina, Chapel Hill, unpublished data). Cummins and Klug (1979) present data for Augusta Creek, Michigan, which document this. Furthermore, variable decay rates of detritus redistribute an apparent pulse of CPOM, such as autumn leaf fall. The input of a few weeks is spread throughout the year, as different leaves become fully conditioned by bacteria and fungi at different rates and therefore become available as food at different times. Minshall (1978) implied that either periphyton, macrophytes, or autochthonously produced detritus is available year-round.

If food is not limiting, then perhaps space is. Primary space (i.e. bare rock) is the limiting resource in the rocky intertidal zone. Dayton (1971) stressed the role of drift logs battering the rocks as creators of new primary space. In streams, major disturbances such as floods and droughts also create new space. Floods will affect all taxa in proportion to their abundance and exposure. This will tend to reduce the population sizes of numerically dominant species. In 1979, New Hope Creek flooded at least six times. In a highly disturbed stream ecosystem, it would be unlikely for competition to proceed to competitive exclusion.

Predation pressure is likely to be a major element in preventing competitive exclusion in streams. In addition to the benthic insect predators discussed here, there are crayfish, salamanders, turtles, water snakes, and fish which all feed on lotic insects. In the New Hope Creek watershed alone, some 50 species of insect predators from Chironomidae to Megaloptera have been identified. Hall (1972) reported 27 species of fish, 4 species of crayfish, 4 turtles, and 2 snakes in New Hope Creek. Given this abundant and diverse predatory fauna, it is possible, even likely, that the effects of predation could offset competition in streams. The mechanism may be analogous to that in the rocky intertidal community.

The factors of abundant resources, frequent disturbances, and intense predation pressure all combine to minimize the role of competition in streams. The patchy, heterogeneous physical environment and the functional groups of species provide opportunity and evidence, respectively, for resource partitioning and niche separation in streams. The high complexity of stream communities can be maintained without competition being a major driving factor. Investigations into the relative contributions of these factors to the maintenance of stream communities in general, and substratum specific associations in particular, are important research objectives for stream ecology.

Acknowledgments

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ALLAN, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56: 1040–1053.

CASWELL, H., H. E. KOENIG, J. A. RESH, AND Q. E. ROSS. 1972. An introduction to systems science for ecologists, p. 3–78. *In* B. C. Patten [ed.] Systems analysis and simulation in ecology. II. Academic Press, New York, NY.

CONNELL, J. H. 1975. Some mechanisms producing structure in natural communities, p. 460–490. *In* M. L. Cody and J. M. Diamond [ed.] Ecology and evolution of communities. Belknap Press, Cambridge, MA.

CUMMINS, K. W., AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: 147–172.

CUMMINS, K. W., AND G. H. LAUFF. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. Hydrobiologia 34: 145–181.

DAYTON, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389.

EGGLISHAW, H. J. 1969. The distribution of benthic invertebrates on substrata in fast flowing streams. J. Anim. Ecol. 38: 19–33.

HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53: 585–604.

HART, D. D. 1978. Diversity in stream insects: regulation by rock size and microspatial complexity. Verh. Int. Ver. Limnol. 20: 1376–1381.

HIGLER, L. W. G. 1975. Reaction of some caddis larvae (Trichoptera) to different types of substrate in an experimental stream. Freshwater Biol. 5: 151–157.

HILDREW, P. G., AND J. M. EDINGTON. 1979. Factors facilitating the coexistence of Hydropsychid caddis larvae (Trichoptera) in the same river system. J. Anim. Ecol. 48: 557–576.

KREBS, C. J. 1978. Ecology: the experimental analysis of distribution and abundance. Harper & Row, Publishers, Inc., New York, NY. 678 p.

LINDUSKA, J. P. 1942. Bottom type as a factor influencing the local distribution of mayfly nymphs. Can. Entomol. 74: 26–30.

MENGE, B. A., AND J. P. SUTHERLAND. 1976. Species diversity gra-

dients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110: 351–369.

MERRITT, R. W., AND K. W. CUMMINS. [ed.] 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co. Dubuque, IA. 441 p.

MINSHALL, G. W. 1978. Autotrophy in streams. BioScience 28: 767–771.

MINSHALL, G. W., AND J. N. MINSHALL. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. Hydrobiologia 55: 231–249.

MOON, H. P. 1939. Aspects of the ecology of aquatic insects. Trans. Br. Soc. Entomol. 6: 39–49.

OBENDORFER, R. Y., J. V. MCARTHUR, AND J. R. BARNES. 1980. The role of predators in the maintenance of leaf pack community structure. Abstract. North American Benthological Society Meeting, Savannah, GA. p. 31.

PAINE, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65–75.

PECKARSKY, B. L. 1979. Biological interactions as determinants of distributions of benthic invertebrates within the substrate of stony streams. Limnol. Oceanogr. 24: 59–68.

1980. Influence of detritus upon colonization of stream invertebrates. Can. J. Fish. Aquat. Sci. 37: 957–963.

1981. Biological interactions revisted. Limnol. Oceanogr. (In press)

PECKARSKY, B. L., AND S. I. DODSON. 1980a. Do stonefly predators influence benthic distributions in streams? Ecology 61: 1275–1282.

1980b. An experimental analysis of biological factors contributing to stream community structure. Ecology 61: 1283–1290.

PIELOU, E. C. 1977. Mathematical ecology. John Wiley & Sons, New York, NY. 385 p.

RABENI, C. F., AND G. W. MINSHALL. 1977. Factors affecting microdistribution of stream benthic insects. Oikos 29: 33–43.

REICE, S. R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. Ecology 55: 1271–1282.

1977. The role of animal associations, current velocity and sediments in lotic litter decomposition. Oikos 29: 357–365.

1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. Ecology 61: 580–590.

ROOT, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol. Monogr. 43: 95–124.

SCOTT, D. 1958. Ecological studies on the Trichoptera of the River Dean, Cheshire. Arch. Hydrobiol. 54: 340–392.

SHELLY, T. E. 1979. The effect of rock size upon the distribution of species of Orthocladiinae (Chironomidae: Diptera) and *Baetis intercalaris* McDunnough (Baetidea: Ephemeroptera). Ecol. Entomol. 4: 95–100.

SHORT, R. A., AND P. E. MASLIN. 1977. Processing of leaf litter by a stream detritivore: effect on nutrient availability to collectors. Ecology 58: 935–938.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw Hill, New York, NY.

ULFSTRAND, S. 1968. Benthic animal communities in lapland streams. A field study with particular reference to Ephemeroptera, Plecoptera, Trichoptera, and Diptera: Simuliidae. Oikos Suppl. 10: 1–120.

VANNOTE, R. L., AND B. W. SWEENEY. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. Am. Nat. 115: 667–695.

WISE, D. H., AND M. C. MOLLES JR. 1979. Colonization of artificial substrates by stream insects: influence of substrate size and diversity. Hydrobiologia 65: 69–74.

Labeling Fish with an Activable Element Through Their Diet

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MICHIBATA, H. 1981. Labeling fish with an activable element through their diet. Can. J. Fish. Aquat. Sci. 38: 1281–1282.

Stable samarium, one of the rare earth elements, was fed to medaka (*Oryzias latipes*) and goldfish (*Carassius auratus*). The concentration of samarium in the labeled fish was determined by neutron activation analysis. In *O. latipes*, samarium was detectable even 1 yr after the labeled diet was eaten. In *C. auratus*, samarium was retained in the fifth branchial arch, scales, and gills.

Key words: fish marking, *Oryzias latipes*, *Carassius auratus*, activation analysis, activable tracer, samarium

MICHIBATA, H. 1981. Labeling fish with an activable element through their diet. Can. J. Fish. Aquat. Sci. 38: 1281–1282.

On a donné en nourriture aux poissons *Oryzias latipes* et *Carassius auratus* du samarium stable, une des terres rares. La concentration de Sm chez les poissons marqués a été mesurée par analyse par activation neutronique. Chez *O. latipes*, Sm a pu être détecté même un an après ingestion du régime marqué. Chez *C. auratus*, Sm a été retenu dans le cinquième arc branchial, les écailles et les branchies.

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MICHIBATA and Hori (1981) have shown that samarium, one of the rare earth elements, administered by injection was suitable for labeling fish, and that samarium was detectable by neutron activation analysis even 2 yr after the last injection. Although injecting samarium is certainly efficient and useful for labeling when the fish are large enough to be handled (Michibata and Hori 1981), administration via diet would be better for either small fish or large numbers of fish.

The following experiments were designed to assess the feasibility of labeling fish with an activable element through their food and to determine in which organ or tissue the element is accumulated.

Materials and methods — Two series of experiments were carried out.

1) Thirty-day-old fry of the medaka, *Oryzias latipes* (about 8.5 mm in mean body length), kept outdoors in an aquarium were used as subjects. Samarium chloride ($SmCl_3 \cdot 6H_2O$) was added directly to the diet (commercial trout food) at the rate of 66 mg of Sm per gram of diet. The fry received the diet for 30 d after which they were reared on the same diet without samarium. It was estimated that 1.3 mg Sm was administered to each fry. The control fry kept in a separate aquarium were fed on the same diet but without samarium throughout the experiment.

Five fish were killed on 1, 30, 60, 90, 120, 150, 180, 240, and 360 d after the labeled diet was eaten for 30 d. They were dried at 110°C for 24 h, and the samarium detected in the fish by neutron activation analysis as described in Michibata and Hori (1981). The control fish were also analyzed for samarium by the same method.

2) Because medaka are too small to determine the site in which samarium is accumulated, the second experiment was carried out using adult goldfish, *Carassius auratus* (about 6 cm in body length). Goldfish were fed the labeled diet (13 mg Sm/g of dry diet) for 40 d, then 20 mg Sm were finally administered to each fish. They afterwards received the same diet without samarium. Five fish were killed on 1, 30, 60, 90, 120, 180, and 360 d after they were fed the labeled diet. After the organs and tissues such as the intestine, liver, gills, scales, and fifth branchial arch were separated, they were also analyzed for samarium.

Results — The diet containing samarium apparently did not harm the fishes during the experiment. As described in Michibata and Hori (1981), a clear photo-peak of ^{153}Sm in the vicinity of 102 keV was recognized in the gamma ray spectrograms of the labeled fish after they were bombarded with thermal neutrons, whereas no distinct photo-peak was ob-

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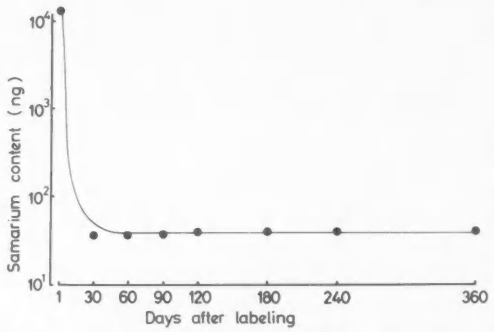

FIG. 1. The change in samarium content of the entire fish after they had eaten a labeled diet for 30 d.

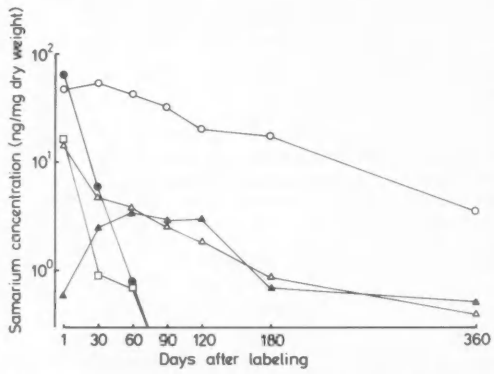

FIG. 2. Changes in the samarium concentration in several organs and tissues of labeled goldfish (expressed as ng Sm/mg of dry weight) after they were fed a labeled diet. (●) Intestine, (□) liver, (○) fifth branchial arch, (△) gills, and (▲) scales.

served in the unlabeled fish throughout the experiment. Since the detection limit of this technique was ~1 ng, the labeled fish were clearly distinguishable from the unlabeled fish.

The amount of samarium decreased dramatically within 30 d after labeling, then the level of samarium detected remained almost constant for the following year (Fig. 1). Thus, it appears that samarium has a relatively long biological half-life in the medaka.

In the intestine and liver of the goldfish the amount of samarium decreased rapidly, and was undetectable by 90 d (Fig. 2). On the other hand, the amount of the element in the fifth branchial arch, scales, and gills tended to decrease but still remained 1 yr after the labeled diet was fed.

Discussion — As mentioned in Michibata and Hori (1981), labeling fish with an activable element offers several advantages: (1) the apparent absence of harmful effects on the fish, (2) the small probability of interference from naturally occurring samarium, (3) the long biological half-life of the deposited samarium, (4) no radioactive contamination of the fish or other organisms, and (5) safety in handling.

Michibata and Hori (1981) found that a large amount of samarium was retained in the internal organs even 2 yr after the intraabdominal injection. There was no marked change in the amount of samarium throughout the experiment. However, in the present experiment, the amount of samarium in the medaka decreased markedly within 30 d after the end of feeding, after which the amount remained constant for 1 yr. These results reflect a distinct difference between administration by feeding and by injection.

Shibuya (1979) reported that salmon, fed europium, another rare earth element, retained the label for 3 mo. He mentioned that the element was deposited mainly in the scales after it was absorbed through the gastrointestinal tract. In mammlas, however, Ellis (1968) and Kennelly et al. (1980) demonstrated that the rare earth elements were not absorbed from the intestine. The retention of considerable samarium in the fifth branchial arch possibly results from adsorption as the fish ingests the labeled diet. Furthermore, samarium deposited in the scales and gills also does not result from absorption through the gastrointestinal tract but from direct absorption from the water where the element is dissolved from the labeled diet or excrement of the fish.

The mechanism of retention of samarium remains to be resolved, but the procedure used in the present experiment can be used to label fish.

Acknowledgments — I am grateful to Professor R. Hori for his helpful comments on this study. Thanks are also due to T. Kibe for his valuable assistance during the course of this experiment.

ELLIS, W. C. 1968. Dysprosium as an indigestible marker and its determination by radioactivation analysis. J. Argic. Food Chem. 16: 220–224.

KENNELLY, J. J., F. X. AHERNE, AND M. J. APPS. 1980. Dysprosium as inter marker for swine digestibility studies. Can. J. Anim. Sci. 60: 441–446.

MICHIBATA, H., AND R. HORI. 1981. Labeling fish with an activable element. Can. J. Fish. Aquat. Sci. 38: 133–136.

SHIBUYA, M. 1979. Non-destructive activation analysis for Eu in fish materials. Radioisotopes 28: 64–68.

Extrathyroidal Effects of Low Concentrations of Thiourea on Rainbow Trout, *Salmo gairdneri*

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EALES, J. G. 1981. Extrathyroidal effects of low concentrations of thiourea on rainbow trout, *Salmo gairdneri*. Can. J. Fish. Aquat. Sci. 38: 1283–1285.

Chronic exposure of fed immature rainbow trout (*Salmo gairdneri*) to a low ambient thiourea (TU) concentration did not depress circulating levels of T_4 (thyroxine) or triiodothyronine, T_4 degradation rate, or T_4 deiodination rate indicating no significant T_4 influence on thyroidal hormone output. However, TU increased the hematocrit and decreased distribution spaces for iodide and T_4, indicating direct sensitivity of extrathyroidal processes to TU.

Key words: thiourea, thyroxine, hematocrit, iodide metabolism, rainbow trout

EALES, J. G. 1981. Extrathyroidal effects of low concentrations of thiourea on rainbow trout, *Salmo gairdneri*. Can. J. Fish. Aquat. Sci. 38: 1283–1285.

Une exposition chronique de truites arc-en-ciel nourries et immatures à une faible concentration de thiourée (TU) ambiante n'abaissa pas les niveaux en circulation de T_4 (thyroxine) ou de triiodothyronine, le taux de dégradation de T_4 ou le taux de désiodation de T_4, ce qui indique que T_4 n'agit pas de façon appréciable sur la production de l'hormone thyroïdienne. Cependant, TU cause une augmentation de l'hématocrite et une diminution des espaces de répartition de l'iode et de T_4, ce qui indique une sensibilité directe à TU des processus extrathyroïdiens.

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THIOUREA (TU) is commonly used to inhibit thyroid function of teleosts (reviewed by Pickford and Atz 1957; Donaldson et al. 1978; Eales 1979). However, apart from the work of Kinnear (1960), Allen and Christy (1978), and Milne and Leatherland (1978), little is known of its mode of action or effectiveness in reducing plasma thyroid hormone levels. For unambiguous interpretation of most experiments involving its use, it is assumed that TU inhibits the thyroid exclusively and exerts no confounding extrathyroidal effects. The possibility of extrathyroidal TU action in teleosts has been recognized (MacKay 1973), but no extrathyroidal actions have been demonstrated to date, although in dogfish, TU inhibition of several branchial and renal enzymes occurs in vitro (Malyusz and Thiemann 1976). In the course of investigating possible effects of TU on the peripheral metabolism of thyroid hormones in rainbow trout, *Salmo gairdneri*, it was observed that a TU concentration too low to inhibit thyroidal secretion of hormone or depress circulating thyroid hormone levels did cause other changes, emphasizing the importance of considering extrathyroidal effects in interpretation of experiments involving TU treatment.

Materials and methods — Immature hatchery-reared rainbow trout were held in two well-aerated 200-L Fiberglass tanks at 11 ± 1°C and fed Ewos trout grower pellets (Astra Chemicals Ltd., Mississauga, Ont.) once each day at a ration of 1% of body weight. The tank containing experimental fish (n = 62) received a water flow of 2 L/min. Thiourea dissolved in 0.1 mol NaOH/L was continually delivered into the inflowing water stream by a peristaltic pump at a rate of 0.3 mL/min to create a calculated ambient TU level of 0.0015%. The control fish (n = 63) received 0.1 mol NaOH/L alone. The NaOH did not measurably alter pH. One control fish died during the experiment. After 67 d exposure to TU or 0.1 mol NaOH/L, 10 experimental and 10 control (C) fish were killed and bled, and plasma T_4 (thyroxine) and T_3 (3,5,3′-triiodothyronine) measured by radioimmunoassay (Brown and Eales 1977). The remaining fish in each tank were injected with Na ^{131}I and [^{125}I]T_4, and plasma radioiodide and radiothyroxine kinetics evaluated. This permitted calculation of plasma T_4DR (degradation rate), fraction of plasma T_4 undergoing deiodination, rate of T_4 to T_3 conversion, enterohepatic T_4 excretion, plasma iodide distribution space, fractional rate of loss of plasma iodide, plasma iodide clearance rate, and thyroid radioiodide uptake (Hunt and Eales 1979a, b). The hematocrit (%) was measured on several subsamples of experimental and control trout by centrifuging heparinized blood in capillary tubes for 5 min in an International HE hematocrit centrifuge.

Results — Thiourea treatment caused no change in body weight (TU = 107 ± 3.3 g ($\bar{x}$ ± SEM); C = 108 ± 2.5 g), plasma T_4 (TU = 2.2 ± 0.2; C = 1.5 ± 0.2 ng·mL^{-1}),

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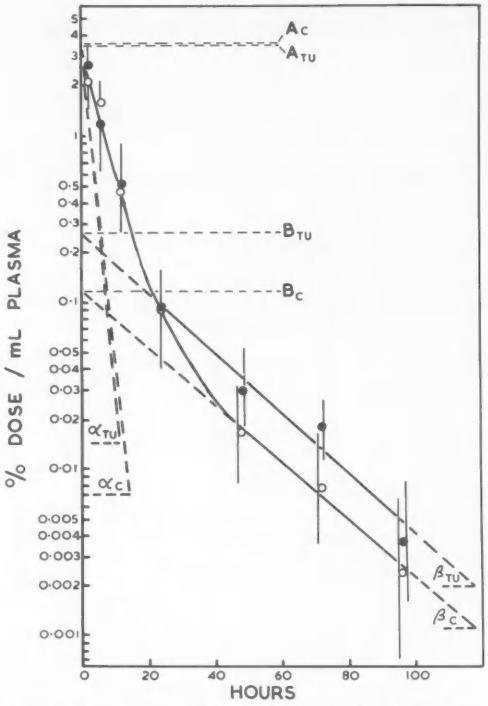

FIG. 1. Disappearance with time of injected [^{125}I]T_4 from plasma of control trout or trout exposed for 63–67 d to TU (0.0015%). Geometric means of 7–10 fish and 95% confidence intervals are plotted at each sampling time. The biphasic exponential curves are peeled into fast and slow components and the equation for each line determined. $C_{control} = 3.43e^{-0.182t} + 0.116e^{-0.04t}$; $C_{thiourea} = 3.63e^{-0.201t} + 0.265e^{-0.043t}$. Covariance analysis of slopes and intercepts of the regressions of fast and slow phases revealed a significantly ($P < 0.01$) greater intercept of the slow component (B) for TU-treated fish than for control fish.

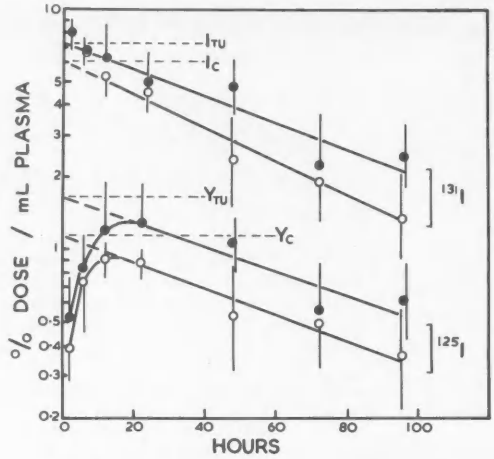

FIG. 2. Plasma levels of $^{125}I^-$ and $^{131}I^-$ at various times afte injection of [^{125}I]T_4 and Na ^{131}I into control rainbow or trout exposed for 63–67 d to TU (0.0015%). Geometric means of 7–10 fish and 95% confidence intervals are plotted at each sampling time. Regressions were based on values from 24 to 96 h inclusive. For $^{125}I^-$ samples the rate constants for $^{125}I^-$ uptake into plasma were determined by subtracting observed $^{125}I^-$ values 2, 6, and 12 h from theoretical values at those times obtained by extrapolation of the $^{125}I^-$ regressions to zero time. This rate constant was then used to correct the respective regression intercept (Y_c or Y_{TU}) for $^{125}I^-$ loss. The ratio of this corrected intercept to the corresponding $^{131}I^-$ intercept (I_c or I_{TU}) provided the fraction of [^{125}I]T_4 undergoing deiodination (Hunt and Eales 1979b).

plasma T_3 (TU = 2.2 ± 0.2; C = 2.2 ± 0.2 ng·mL^{-1}), T_4DR (TU = 9.6; C = 7.0 ng·h^{-1}·100 g^{-1}), fraction of plasma T_4 deiodinated (TU = 0.34; C = 0.29), fractional rate of loss of plasma iodide (TU = 0.012; C = 0.016 h^{-1}), enterohepatic T_4 loss or thyroid radioiodide uptake. However, TU treatment did cause (i) a small but significant ($P < 0.05$) increase in hematocrit (TU = 39.6 ± 0.89; C = 36.6 ± 0.87%), (ii) a significant ($P < 0.01$) elevation of the intercept of the regression for the slow component depicting [^{125}I]T_4 loss from plasma (Fig. 1), indicating a decrease in T_4 distribution space, and (iii) a significant ($P < 0.005$) elevation of the intercept of the regressions for the loss of plasma $^{125}I^-$ or $^{131}I^-$ (Fig. 2), indicating a decrease in plasma iodide distribution space (TU = 13.9; C = 16.6 mL·100 g^{-1}), and resulting in a decrease in plasma iodide clearance (TU = 0.17; C = 0.27 mL·h^{-1}).

Discussion — Thiourea treatment did not depress significantly circulating levels of T_4 or T_3, T_4 degradation rate or peripheral T_4 deiodination, and it is concluded that there was no reduction in the synthesis or release of hormone from the thyroid or availability of T_4 or T_3 to tissue receptor sites in trout. Thyroid radioiodide uptake was lowered somewhat but not significantly ($P > 0.05$), indicating that under conditions used, a TU concentration of 0.0015% may be close to the threshold for influencing the thyroid. In support of this, Kinnear (1960) found that in starry flounder (*Platichthys stellatus*) the lowest effective TU dose inhibiting synthesis of labeled T_4 was 0.0025%; Chua and Eales (1972) observed significant depression in thyroid radioiodide uptake in brook trout (*Salvelinus fontinalis*) at a TU concentration of 0.001%. However, higher TU doses may be required to depress circulating thyroid hormones. In rainbow trout Allen and Christy (1978) found that 19-d treatment with 5 mmol TU did not depress plasma T_4, while in the same species Milne and Leatherland (1978), although demonstrating a statistically significant reduction with intermittent use of a high TU dose (0.1%) over 15 d, were unable to depress plasma T_4 and T_3 substantially.

Despite the undiminished T_4DR and unaltered circulating levels of T_4 and T_3 in TU-treated trout, the hematocrit increased significantly while the distribution spaces for T_4 and iodide decreased. It is concluded, therefore, that these parameters were influenced directly by TU and did not depend on any alteration in thyroidal status. These changes assume greater physiological significance when it is remembered that

the TU levels used in the present study were 20–667 × lower than the levels (0.03–1.0%) used in numerous (~30) previous studies on fish. Assuming that the trout is reasonably representative of other teleosts, and assuming that TU effects increase with dose, it is predicted that considerable extrathyroidal TU may have occurred in earlier work. However, the extent to which extrathyroidal TU action may have confounded previous interpretations remains to be determined. One way to compensate for extrathyroidal TU action is to compare TU-treated fish with TU-treated fish also treated with thyroid hormones (Sage 1968). This rarely used approach is recommended for future experiments involving TU and possibly other goitrogens.

The extrathyroidal effects described in this study may be related and stem from some common TU action. For example, the increase in hematocrit and decrease in distribution spaces for iodide and T_4 could be explained by hemoconcentration which stems from alteration in water/electrolyte balance between blood and other fluid compartments.

It should be emphasized that the original purpose of this study was to determine if TU influenced the peripheral metabolism of thyroid hormones or iodide and no attempt was made to monitor other parameters that might be directly susceptible to TU influence.

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ALLEN, D. M., AND M. CHRISTY. 1978. Thiourea does not block visual pigment responses to prolactin in a trout. Vision Res. 18: 859–860.

BROWN, S. B., AND J. G. EALES. 1977. Measurement of L-thyroxine and 3,5,3′-triiodo-L-thyronine levels in fish plasma by radioimmunoassay. Can. J. Zool. 55: 293–299.

CHUA, D., AND J. G. EALES. 1971. Thyroid function and dermal purines in the brook trout, *Salvelinus fontinalis* (Mitchill). Can. J. Zool. 49: 1557–1561.

DONALDSON, E. M., U. H. M. FAGERLUND, D. A. HIGGS, AND J. R. MCBRIDE. 1978. Hormonal entrancement of growth in fishes, p. 456–597. *In* W. S. Hoar and D. J. Randall [ed.] Vol 8. Academic Press, New York and London.

EALES, J. G. 1979. Thyroid functions in cyclostomes and fishes, p. 341–436. *In* E. J. W. Barrington [ed.] Hormones and evolution. Vol. 1. Academic Press, New York, NY.

HUNT, D. C. W., AND J. G. EALES. 1979a. The influence of testosterone propionate on thyroid function of immature rainbow trout, *Salmo gairdneri*, Richardson. Gen. Comp. Endocrinol. 37: 115–121.

1979b. Iodine balance in rainbow trout (*Salmo gairdneri*) and effects of testosterone propionate. J. Fish. Res. Board Can. 36: 282–285.

KINNEAR, J. E. 1960. The minimum dosage of thiourea effectively inhibiting thyroxine synthesis in the flounder (*Platichthys stellatus*). Can. J. Zool. 38: 917–922.

MACKAY, N. J. 1973. The effects of methallibure (I.C.I. 33,383) and thiourea on gametogenesis in the fire-tail gudgeon, *Hypseleotris galli*. Gen. Comp. Endocrinol. 20: 221–235.

MALYUSZ, M., AND V. THIEMANN. 1976. The effect of urea, thiourea and acetamide on the renal and branchial enzyme pattern of the dogfish *Scyliorhinus canicula*. Comp. Biochem. Physiol. 54B: 177–179.

MILNE, R. S., AND J. F. LEATHERLAND. 1978. Effect of ovine TSH, thiourea, ovine prolactin and bovine growth hormone on plasma thyroxine and triiodothyronine levels in rainbow trout (*Salmo gairdneri*). J. Comp. Physiol. 124: 105–110.

PICKFORD, G. E., AND J. W. ATZ. 1957. The physiology of the pituitary gland of fishes. New York Zoological Society, New York, NY. 613 p.

SAGE, M. 1968. Respiratory and behavioural responses of *Poecilia* to treatment with thyroxine and thiourea. Gen. Comp. Endocrinol. 10: 304–309.

Sterilization of Sea Lampreys (*Petromyzon marinus*) by Immersion in an Aqueous Solution of Bisazir[1]

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HANSON, L. H. 1981. Sterilization of sea lampreys (*Petromyzon marinus*) by immersion in an aqueous solution of bisazir. Can. J. Fish. Aquat. Sci. 38: 1285–1289.

Groups of sea lamprey (*Petromyzon marinus*) eggs fertilized by males previously immersed in an aqueous solution of *p,p*-bis(1-aziridinyl)-*N*-methylphosphinothioic amide (bisazir) at concentrations of 10–100 mg/L produced fewer normal, live prolarvae after 15–17 d of incubation than did groups of eggs fertilized by normal males. Mortality of embryos or prolarvae was nearly 100% in groups of eggs fertilized by males that had been

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immersed in a 50 mg/L solution of bisazir for 4 h or in a 100 mg/L solution for 2 h. The immersion technique appears to be an efficient method of sterilizing large numbers of male sea lampreys for use in a proposed sterile-male-release program.

Key words: sea lamprey, *Petromyzon marinus*; pest control, fish control, sterile-male technique, sterilization, chemosterilants, bisazir, Great Lakes

HANSON, L. H. 1981. Sterilization of sea lampreys (*Petromyzon marinus*) by immersion in an aqueous solution of bisazir. Can. J. Fish. Aquat. Sci. 38: 1285–1289.

Des groupes d'œufs de grande lamproie marine (*Petromyzon marinus*) fécondés par des mâles auparavant immergés dans une solution aqueuse de *p,p*-bis(1-aziridinyl)-*N*-méthylphosphinothioique amide (bisazir) à des concentrations variant de 10 à 100 mg/L produisent moins de prolarves vivantes normales après 15–17 jours d'incubation que des groupes d'œufs fécondés par des mâles normaux. Les mortalités d'embryons ou de prolarves sont de près de 100% dans des groupes d'œufs fécondés par des mâles qui avaient été immergés dans une solution de 50 mg/L de bisazir pendant 4 h ou dans une solution de 100 mg/L pendant 2 h. La technique d'immersion semble être une méthode efficace de stérilisation de grands nombres de lamproies marines mâles dans le programme proposé de libération de mâles stériles.

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SELECTIVE toxicants (Applegate et al. 1961; Howell et al. 1964; Manion 1969) have been used successfully to control populations of the sea lamprey (*Petromyzon marinus*) in the Great Lakes. Treatments of larval populations in streams tributary to Lake Superior have reduced lamprey abundance in Lake Superior by about 90%, and similar reductions are believed to have occurred in Lakes Huron and Michigan (Smith and Tibbles 1980). Although selective toxicants have been used successfully, other methods of control are needed for an effective integrated control program. One method receiving considerable attention in pest control programs is the sterility technique first proposed by E. F. Knipling (1955). Many of the principles involved in insect population control by the release of sterile insects, discussed by Knipling (1964, 1968), are also applicable to the control of vertebrate pests. A basic requirement for employing the sterile-male-release technique is the availability of a method of inducing sterility which has no serious adverse effect on the mating behavior and competitiveness of the sterilized male.

The recent discovery of a chemosterilant for sea lampreys (Hanson and Manion 1978) offers the prospect of an additional method of control of this pest. Laboratory tests showed that *p,p*-bis(1-aziridinyl)-*N*-methylphosphinothioic amide[2] (bisazir), dissolved in 0.9% saline to produce a 10 000 mg/L stock solution and injected intraperitoneally at a dosage of 100 mg/kg, sterilized spawning-run sea lampreys. Although sperm from sterilized males successfully fertilized eggs, complete mortality occurred before they developed to the larval stage (stage 18 of Piavis 1961). Field tests conducted in 1974 and 1976 on experimental populations of spawning adults established in an isolated portion of the Big Garlic River, Marquette County, MI, confirmed that the injection of male sea lampreys with bisazir resulted in their sterilization. The field studies also showed that the injection of bisazir had no apparent effect on nest building, spawning behavior, or mating competitiveness of the sterilized lampreys (Hanson and Manion 1978, 1980).

Because injecting individual lampreys with bisazir is time consuming, I attempted to develop a method for sterilizing male spawning-run sea lampreys by immersing them in an aqueous solution of bisazir.

Materials and methods — In 1977 and 1978, spawning-run sea lampreys were collected in May from the Cheboygan River, Cheboygan County, MI, and transferred to a concrete holding tank at the Hammond Bay Biological Station. In late June, male lampreys (average weight 212 g; range 132–344 g) were removed from the holding tank, acclimated to the

TABLE 1. Treatments of male sea lampreys placed in an artificial stream, and number artificially spawned in 1977 and 1978 during studies of sterilization by immersion.[a]

Treatment			
Concn. of bisazir (mg/L)	Time of immersion (h)	No. of lampreys	No. observed spawning and artificially spawned
10	4	20	10
25	4	10	7
50	2	10	6
50	4	10	7
100	2	10	6
0	0	50	30[b]

[a]A total of 55 untreated females were placed in the stream.
[b]When insufficient numbers of normal spawning males were available to provide a separate control for each batch fertilized by a treated male, sperm from two treated males and a normal male was used to fertilize three batches of eggs from the same female.

[2]This compound (USDA code number A13-61585) was obtained from A. B. Borkovec, U.S. Department of Agriculture, Insect Reproduction Laboratory, Beltsville, MD 20705.

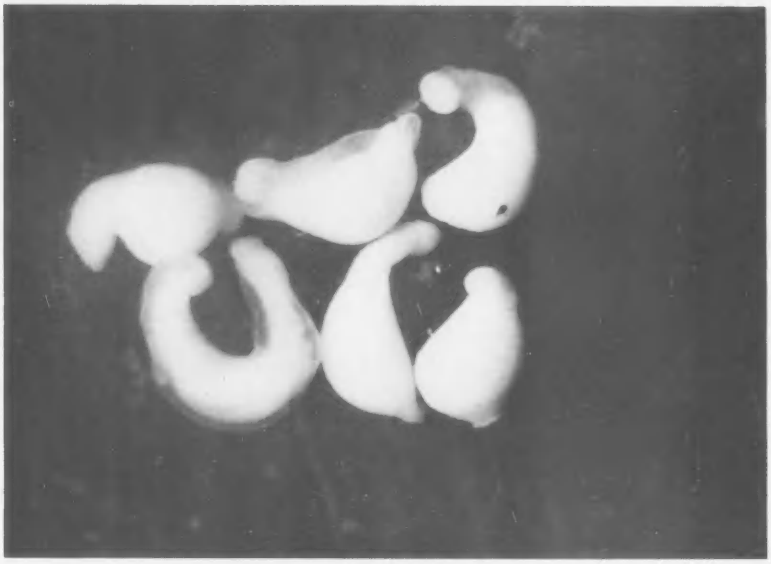

FIG. 1. Abnormal sea lamprey embryos (16 d old) produced by fertilizing eggs with sperm from a male that had been immersed in 100 mg/L aqueous solution of bisazir for 2 h.

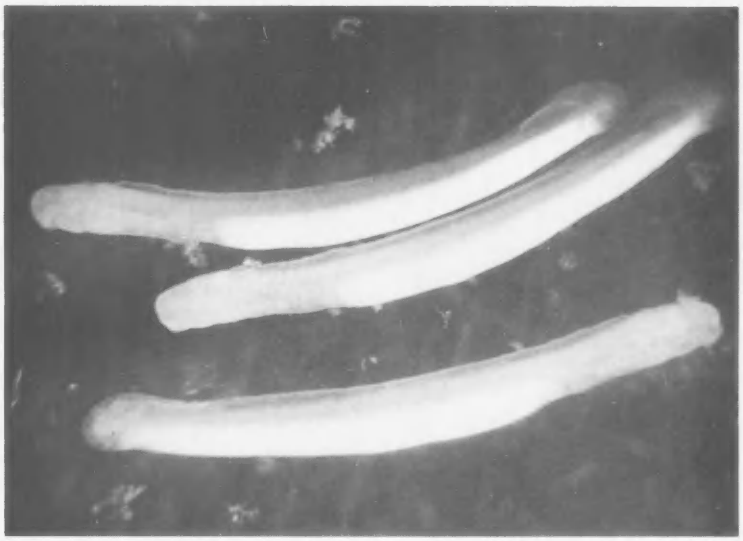

FIG. 2. Normal, stage 16 (Piavis 1961) sea lamprey embryos (16 d old) produced by fertilizing eggs with sperm from an untreated male. Same female used as source of eggs for embryos seen in Fig. 1.

test temperature of 12.8°C, and placed in various test solutions of bisazir for 2 or 4 h (Table 1).

Test solutions were made by dissolving bisazir in 20 L of Lake Huron water. However, 40 L of test solution was used in the test concentration of 10 mg/L because twice as many lampreys were immersed in this solution as in the others. All

TABLE 2. Effects of immersion of male sea lampreys in aqueous solutions of bisazir on the production of normal prolarvae after 15–17 d of incubation when treated males were artificially spawned with untreated females. Normal females were also spawned with normal males to provide controls on the fertility of the females.

Treatment of males[a]				Average percentage per spawning (ranges in parentheses)		
Concn. of bisazir (mg/L)	Duration (h)	No. spawned artificially	Avg. no. of eggs per spawning (ranges in parentheses)	Dead	Live, abnormal prolarvae	Live, normal prolarvae
10	4	10	816 (154–1880)	63.5 (21.4–97.4)	14.5 (2.0–29.9)	22.1 (0.0–56.1)
0	0	10	655 (258–1469)	22.9 (14.1–43.0)	4.5 (0.7–14.3)	72.6 (42.6–82.9)
25	4	7	1382 (737–2339)	93.1 (75.4–100.0)	4.9 (0.0–17.7)	2.0 (0.0–6.9)
0	0	7	1382 (858–1855)	24.5 (4.1–79.6)	3.8 (0.8–12.5)	71.7 (19.1–95.2)
50	2	6	1158 (542–2074)	84.7 (37.8–98.5)	11.0 (1.0–43.9)	4.3 (0.5–18.3)
0	0	6	1164 (620–1855)	46.7 (11.9–97.6)	3.1 (0.7–9.4)	50.2 (1.8–86.2)
50	4	7	1800 (1290–2643)	98.2 (94.4–100.0)	1.6 (0.0–5.2)	0.2 (0.0–0.6)
0	0	7	1371 (1112–1717)	32.8 (3.6–88.5)	4.2 (0.1–12.3)	63.0 (4.9–95.5)
100	2	6	1077 (294–2707)	99.7 (98.9–100.0)	0.3 (0.0–0.8)	0.1 (0.0–0.3)
0	0	6	919 (265–1873)	27.6 (20.0–39.8)	3.4 (0.6–4.9)	69.1 (59.6–75.1)

[a]Zero treatment concentrations and durations identify the controls for the accompanying treatment groups.

test solutions were made up in 57-L aquariums which were partly immersed in a constant temperature water bath held at 12.8°C. Oxygen levels were maintained near saturation by aerating the water with stone air breakers.

Immersion of lampreys in the bisazir solution anesthetized them. In the 10 mg/L solution, the lampreys were anesthetized after 2 h; at higher concentrations all lampreys were anesthetized within 5 min. After the lampreys were removed from the bisazir solutions they were fin clipped for identification and placed in an artificial stream in the laboratory (Hanson and Manion 1978). No lampreys died while in the bisazir solutions and all recovered from the anesthetic effect of bisazir after a few hours in fresh water. Normal, spawning-run males and females (unexposed to test solutions) were also placed in the stream.

Lampreys in the artificial stream were observed periodically from 08:00 to 16:30 and those observed in the spawning act were removed from the stream and artificially spawned. One portion of the eggs stripped from each female was fertilized with sperm from a bisazir-treated male; a second portion was fertilized with sperm from an untreated male to provide a control. When insufficient numbers of normal spawning males were available to provide a separate control for each batch of eggs fertilized by a treated male, sperm from two treated males and a normal male was used independently to fertilize three batches of eggs from the same female.

To facilitate care and handling of the embryos and prolarvae, only a small portion of the total number of eggs from each female were kept. Eggs were placed in 10-L glass battery jars (250 mm in diameter) containing 6 L of Lake Huron water. The jars were partly immersed in a constant temperature water bath held at 18.3°C, optimum for the development of sea lamprey embryos (Piavis 1961). The water was changed frequently, dead eggs, embryos, and prolarvae were removed and counted when detected, and oxygen levels were maintained near saturation with an air bubbler. After 15–17 d of incubation, the study was terminated and the remaining dead (disintegrating) prolarvae, the live, normal prolarvae, and the live, abnormal prolarvae were counted. Live prolarvae judged to be abnormal were usually so grossly deformed that survival was considered to be highly improbable (Fig. 1). All live, normal prolarvae were in stages 15 or 16 (Fig. 2). Stages 1–13 designate the embryos from zygotes to hatching (stage 14), and stages 15 (pigmentation) and 16 (gill-cleft formation) designate the prolarvae until they leave the nest and burrow in the bottom mud (stage 17) (Piavis 1961).

Results and discussion — The immersion of male lampreys in the aqueous solutions of bisazir had no noticeable effect on their nest building or spawning behavior. Between 50 and 70% of the males exposed to each concentration of bisazir were observed spawning in the artificial stream whereas 60% of the normal males were observed spawning (Table 1). These percentages undoubtedly would have been higher if continuous observations of the spawning activity in the stream had been possible.

The immersion of male lampreys in aqueous solutions of bisazir greatly reduced the survival rate of normal prolarvae at all concentrations and immersion times tested (Table 2). In

all tests, the survival of normal prolarvae after 15–17 d of incubation was markedly lower in the experimental lots than in their corresponding controls. The average survival of both normal and abnormal prolarvae was higher in groups of eggs fertilized by males subjected to a concentration of 50 mg/L of bisazir for 2 h than in those fertilized by males immersed in a 25 mg/L solution for 4 h. Nearly complete sterility occurred among males immersed in a 50 mg/L solution of bisazir for 4 h or in a 100 mg/L solution for 2 h. Of the eggs fertilized with sperm from six males immersed in a 100 mg/L solution for 2 h, three groups yielded no live prolarvae (normal or abnormal), two groups only a total of nine abnormal prolarvae, and the remaining group yielded seven abnormal and three normal, live prolarvae.

The study showed that immersion in an aqueous solution of bisazir sterilizes spawning-run male lampreys. Although complete sterility did not occur at any of the concentrations or immersion times tested, either a higher concentration of bisazir (>100 mg/L) or longer exposure time at 100 mg/L (>2 h) could be expected to cause complete sterility.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1. 35 p.

HANSON, L. H., AND P. J. MANION. 1978. Chemosterilization of the sea lamprey (*Petromyzon marinus*). Great Lakes Fish. Comm. Tech. Rep. 29. 15 p.

1980. Sterility method of pest control and its potential role in an integrated sea lamprey (*Petromyzon marinus*) control program. Can. J. Fish. Aquat. Sci. 37: 2108–2117.

HOWELL, J. H., E. L. KING JR., A. J. SMITH, AND L. H. HANSON. 1964. Synergism of 5,2′-dichloro-4′-nitro-salicylanilide and 3-trifluormethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8. 21 p.

KNIPLING, E. F. 1955. Possibilities of insect control or eradication through the use of sexually sterile males. J. Econ. Entomol. 48: 459–462.

1964. The potential role of the sterility method for insect population control with special reference to combining this method with conventional methods. U.S. Dep. Agric. Res. Serv. ARS-33-98. 54 p.

1968. The potential role of sterility for pest control, p. 7–40. *In* G. C. LaBrecque and C. N. Smith [ed.] Principles of insect chemosterilization. Appleton-Century-Crofts, New York, NY.

MANION, P. J. 1969. Evaluation of lamprey larvicides in the Big Garlic River and Saux Head Lake. J. Fish. Res. Board Can. 26: 3077–3082.

PIAVIS, G. W. 1961. Embryological stages in the sea lamprey and effects of temperature on development. U.S. Fish Wildl. Serv. Fish. Bull. 61: 111–143.

SMITH, B. R., AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

SETCOL — A Technologically Simple and Reliable Method for Measuring Phytoplankton Sinking Rates

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BIENFANG, P. K. 1981. SETCOL — A technologically simple and reliable method for measuring phytoplankton sinking rates. Can. J. Fish. Aquat. Sci. 38: 1289–1294.

A simple and reliable method for measuring the sinking rate of phytoplankton is described. This technique is suitable for both heterogeneous field populations and unialgal in vitro cultures. The procedure involves use of settling columns initially containing a uniformly mixed population of cells, and calculates a sinking rate based upon the change in vertical distribution of cells after a given time. The sinking rate calculation, though simple, is couched within a sound theoretical foundation. The biomass index used is optional and can be selected to focus on various parameters of interest. Sinking rates and flux values for particulate C, N, P, Si, chlorophyll, or pheopigment can be obtained simply by assessment of the biomass variables in those terms.

Key words: phytoplankton, sinking, methodology, particulate flux, sedimentation

BIENFANG, P. K. 1981. SETCOL — A technologically simple and reliable method for measuring phytoplankton sinking rates. Can. J. Fish. Aquat. Sci. 38: 1289–1294.

L'article qui suit contient une description d'une méthode simple et fiable de mesure des taux de chute du phytoplancton. Cette méthode convient à la fois à des populations hétérogènes sur le terrain et à des cultures monoalgales in vitro. On se sert de colonnes de sédimentation contenant initialement une population de cellules uniformément mélangées, et

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on calcule le taux de chute d'après le changement de distribution verticale des cellules en un temps déterminé. Le calcul du taux de chute, quoique simple, repose sur une base théorique solide. L'indice de biomasse utilisé est facultatif et on peut le choisir pour mettre l'accent sur divers paramètres d'intérêt. On peut déterminer les taux de chute et les valeurs d'écoulement de C, N, P, Si, chlorophylle ou phaeopigment particulaires simplement par évaluation en ces termes des variables de la biomasse.

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OVER the years a number of methodological approaches have been developed to measure the sinking rates of phytoplankton. These have included (a) the visual counting of cells using an inverted microscope (e.g. Smayda and Boleyn 1965, 1966a, b); (b) optical density measurements using a spectrophotometer (Steele and Yentsch 1960); (c) fluorometric methods measuring in vivo chlorophyll (Eppley et al. 1967; Titman 1975; Anderson and Sweeney 1977, 1978; Bienfang et al. 1977; Bienfang 1980); (d) detection of radioactively [^{14}C] labeled cells (Rothwell and Bienfang 1978; Bienfang 1979, 1980); and (e) use of sedimentation tubes (Lännergren 1979). Discussion of the advantages, shortcomings, applicable conditions, and underlying assumptions of such methods are given in Eppley et al. 1967, Smayda 1970, Titman 1975, and Bienfang et al. 1977. With the exceptions of the radiocarbon and sedimentation tube methods, earlier approaches share the shortcoming of being unsuitable for the analysis of natural phytoplankton populations. The method described below has been under evaluation for more than 2 years. Its development was fostered in part by an awareness that the complex ^{14}C technique, while effective, presents imposing technological difficulty for general use by others interested in sinking. The purposes of this communication are (a) to describe this method's design, mode of operation, and calculation of the mean sinking rate; (b) to explain the mean sinking rate calculation in the context of the underlying theory, and (c) to demonstrate the comparability of values so obtained with those acquired by other methods.

The method (termed SETCOL) is a member of the homogeneous sample family of methods (Bienfang et al. 1977). The procedure involves the use of settling columns of known height, initially containing a uniform distribution of cells, and calculates the population's mean sinking rate, ψ, based upon the change in vertical distribution of biomass after a given time. The sinking rate calculation, although simple, is based on a sound theoretical foundation. This method centers on acquisition of ψ from the net change in sample biomass distribution within the column after a finite time, t; this focus is unique from other methods that rely on an analysis of the time derivative of biomass change. This change of focus results in substantially increased simplicity in procedure, and avoids several areas of error which potentially may be incurred in time-derivative approaches.

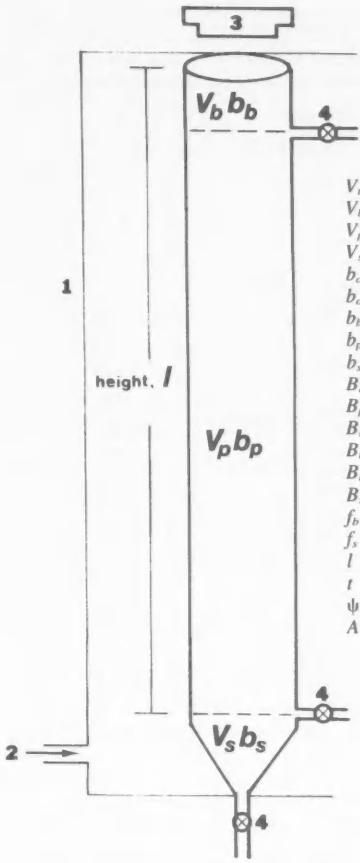
Results — Column design — A diagram of the settling column is given in Fig. 1 together with identification of symbols to be used in this discussion. The column consists of a Plexiglas cylinder equipped with ports for subsample removal; the cylinder is fused at the bottom to a funnel made from a bored piece of Plexiglas stock. A snugly fitting, bored Plexiglas cap fits in the cylinder top to remove free surface area and enhance column stability. These columns are set within a water jacket constructed of clear 6.4-mm-Plexiglas sheets; temperature control for the maintenance of hydrostatic conditions is attained by water circulation driven by a thermostatically controlled water bath. For work with in vitro populations, I used columns having height, diameter, and volume dimensions of 50 cm, 3 cm, and 350 mL, respectively, with positioning of the sampling ports to provide subsample volumes V_b, V_s (for the buoyant and settled fractions, respectively) of about 25 mL each. For work with natural populations when low standing stocks necessitate larger subsample volumes, I used columns of ~9-cm diameter and 4-L volume, which give subsample volumes (V_b, V_s) of about 300 mL.

Procedure — The method yields both sinking rate and ascent rate values from changes in the vertical distribution of biomass which occur in the column after a given period of time; this is shown schematically in Fig. 2. Figure 2A shows the uniform biomass distribution throughout the column at the beginning of a trial; Fig. 2B illustrates the net change in biomass distribution resulting from the population sinking and/or ascent over the duration of the trial.

The first step in conducting a trial by this method is to determine the initial biomass concentration ($b_{o,o}$) of the sample at hand and to fill the column with sample. A tight-fitting cap is placed on the column to remove free surface area, thus inhibiting water motion. The column is then allowed to sit for several hours under the environmental conditions of choice. Upon termination of a trial, a second biomass determination ($b_{o,t}$) is made on an aliquot of the original sample (i.e. $b_{o,o}$) which has been kept outside of the column under identical conditions. The purpose of this measurement is to account for any biomass changes during the trial due to processes other than sinking. Both $b_{o,o}$ and $b_{o,t}$ estimates are made in duplicate, and experience shows that the difference between the means is usually within analytical variability. The total biomass (B_t, in μg) within the entire column is given by the product of the mean concentration (in μg/mL) and the total column volume (V_t, in mL):

$$(1) \quad B_t = \tfrac{1}{2}(b_{o,o} + b_{o,t})\, V_t.$$

During the trial, biomass within the lower region (V_s) and the upper region (V_b) progressively accumulates as a result of sinking and positive buoyancy, respectively. Upon completion of the trial, the upper V_b region is slowly decanted by gradually opening a valve to allow flow (<50 mL$\cdot$min^{-1}) through a side port; the V_b volume is then precisely measured,



V_t = Total volume of sample in SETCOL (= $V_b + V_p + V_s$)
V_b = Volume of upper column region
V_p = Remaining volume above V_s
V_s = Volume of settled region
$b_{o,o}$ = Whole sample concentration at start of trial (e.g. in μg/L)
$b_{o,t}$ = Whole sample concentration at end of trial
b_b = Biomass concentration in V_b at end of trial
b_p = Biomass concentration which remained suspended during trial
b_s = Biomass concentration in V_s at end of trial
$B_{o,o}$ = Total biomass initially within the SETCOL (= $b_{o,o}V_t$)
B_p = Total biomass remaining in suspension after trial (= $V_p b_p$)
$B_{o,t}$ = Total sample biomass, analyzed at the end of the trial (= $b_{o,t}V_t$)
B_t = Total biomass within SETCOL volume [= $\frac{1}{2}(B_{o,o} + B_{o,t})$]
B_b = Total buoyant biomass (= $b_b V_b$)
B_s = Total biomass settled during trial time t [= $V_s b_s - V_s(b_{o,o} + b_{o,t})/2$]
f_b = Fraction that ascended to V_b during trial time t (= B_b/B_t)
f_s = Fraction that sank during the trial time t (= B_s/B_t)
l = Height of sinking column
t = Duration of trial
ψ = Mean sinking rate of biomass (= $f_s \cdot l/t$) (in $m \cdot d^{-1}$)
A = Mean ascent rate of biomass (= $f_b \cdot l/t$) (in $m \cdot d^{-1}$)

FIG. 1. SETCOL apparatus and symbols for discussion.

and the contents are filtered. The biomass concentration (b_b) times the volume (V_b) gives the amount of biomass (B_b, in μg) in the region upon termination. The B_b value is then corrected for sinking losses from the original condition (i.e., $V_b b_o$) by subtraction of an expression giving the fraction of the original biomass ($V_b b_o$) in the V_b region which would sink out, based upon the sinking rate (ψ) value calculated later. The buoyant biomass (B_b, in μg) is given by

$$(2) \quad B_b = V_b b_b - (1 - t\psi/l_b)\,[V_b(b_{o,o} + b_{o,t})/2]$$

where t is the trial duration and l_b is the length of the V_b region. In the strictest mathematical terms, validity of this equation requires that the positively buoyant population fraction be much less than the negatively buoyant fraction, and experience with a wide variety of in vitro and in vivo populations has shown that this is invariably the case.

The fraction of the total biomass in the column which was positively buoyant ($f_b = B_b/B_t$) is used together with the total column height, l, and elapsed time of the trial, t, to give the ascent rate, A (in $m \cdot d^{-1}$) of the population according to the algebraic equation

$$(3) \quad A = (B_b/B_t)l/t = \frac{V_b b_b - (1 - t\psi/l_b)(V_b(b_{o,o} + b_{o,t})/2)}{V_t(b_{o,o} + b_{o,t})/2}\,(l/t).$$

The remaining column volume (V_p) above the V_s region, containing biomass which remained suspended over the course of the trial, is then slowly decanted by gradually opening a valve to allow flow through the lower side port (Fig. 1). This leaves the unperturbed settled volume (V_s) containing the settled biomass (B_s). The settled region (V_s) is lightly scraped from above with a long-handled rubber policeman (e.g. a pipet bulb attached to a glass rod) and the V_s sample contents are decanted through the funnel bottom; the V_s volume is then measured and the contents are filtered along with a rinse of the V_s region. The amount of biomass ($V_s b_s$) in

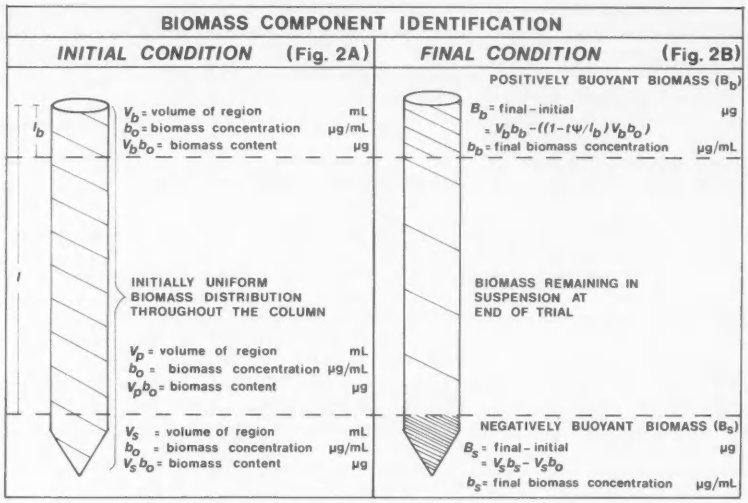

BIOMASS COMPONENT IDENTIFICATION
INITIAL CONDITION (Fig. 2A)
FINAL CONDITION (Fig. 2B)
POSITIVELY BUOYANT BIOMASS (B_b)
V_b = volume of region mL
b_o = biomass concentration µg/mL
$V_b b_o$ = biomass content µg
B_b = final − initial µg
= $V_b b_b - ((1 - t\psi/l_b) V_b b_o)$
b_b = final biomass concentration µg/mL
l_b
l
INITIALLY UNIFORM BIOMASS DISTRIBUTION THROUGHOUT THE COLUMN
BIOMASS REMAINING IN SUSPENSION AT END OF TRIAL
V_p = volume of region mL
b_o = biomass concentration µg/mL
$V_p b_o$ = biomass content µg
V_s = volume of region mL
b_o = biomass concentration µg/mL
$V_s b_o$ = biomass content µg
NEGATIVELY BUOYANT BIOMASS (B_s)
B_s = final − initial µg
= $V_s b_s - V_s b_o$
b_s = final biomass concentration µg/mL

FIG. 2. Biomass separation in SETCOL chambers. Hatch marks indicate biomass density. All symbol identification given in Fig. 1. The mean sinking rate (ψ) and ascent rate (A) necessary to effect the observed final biomass distribution is given by $\psi = (B_s/B_t)l/t$ and $A = (B_b/B_t)l/t$, respectively.

this region is corrected for the amount present at the trial onset $[\frac{1}{2}(b_{o,o} + b_{o,t})V_s]$ to give the net biomass (B_s, in µg) which settled during the trial:

$$(4) \quad B_s = V_s b_s - \tfrac{1}{2}(b_{o,o} + b_{o,t})\, V_s.$$

Equation 4 assumes that any positively buoyant biomass originally in the V_s region is negligible; this is a valid assumption since both $f_b << f_s$ and $V_s << V_t$ and therefore $f_b V_s << f_s V_t$.

The net fraction of the total biomass which was negatively buoyant ($f_s = B_s/B_t$) is used together with the total column height, l, and elapsed trial time, t, to give the mean sinking rate, ψ, of the population according to the equation

$$(5) \quad \psi = (B_s/B_t)\, l/t = \frac{(V_s b_s - V_s(b_{o,o} + b_{o,t})/2)}{V_t(b_{o,o} + b_{o,t})/2}\,(l/t).$$

Theoretical background — The sinking rate calculation, although simple, is based on a sound theoretical framework describing settling losses from a homogeneously mixed column (Bienfang et al. 1977). For a vertical tube filled with sample containing an initially uniform distribution of biomass (Fig. 1, 2A), consider cells initially at a distance x above the bottom region V_s; in order to sink out of the upper region into V_s by time t, these cells must have a sinking rate $v \geq x/t$. Therefore the fraction f_x of cells initially at distance x above the V_s region which will have sunk out by time t is given by

$$(6) \quad f_x = \int_{x/t}^{\infty} \rho(v)dv.$$

Averaging f_x over all values of x in the tube gives the fraction of biomass f_s vertically distributed throughout the tube which will have sunk out by time t; this is given by

$$(7) \quad f_s = l^{-1} \int_0^l dx \int_{x/t}^{\infty} \rho(v)dv.$$

If the order of integration over the dummy variables x and v is reversed, it becomes

$$(8) \quad f_s = (t\psi/l) - \int_{x/t}^{\infty} [(tv/l) - 1]\rho(v)dv,$$

where ψ is the mean sinking rate $\psi = \int_0^{\infty} v\rho(v)dv$. The integral $\int_{x/t}^{\infty} [(tv/x) - 1]\, \rho(v)dv = 0$ if no cells sink faster than l/t, and it has a negligible effect on ψ for even somewhat longer periods than t, because the distribution of specific sinking velocities in populations shows an exponential-type decline in cohort fractions having rates considerably greater than the mean.

It is clear from the equation that a plot of f_s versus time should be initially linear (since no cells have infinite sinking rates), and will remain linear until such time as the integral term becomes substantially nonzero. Empirical evidence of this linearity is described (Fig. 3) over a range of f_s and t values from a number of trials. The test population was a steady-state culture of *Ditylum brightwelli*, growing under NO_3^--limitation at a specific growth rate of 0.020 h^{-1}. This culture was grown under conditions of continuous light (1.5×10^{16} quanta·cm^{-2}·s^{-1}) at a temperature of 23°C and had a cell density of 3000 cells·mL^{-1}. Thus, just as the mean sinking rate can be determined from the slope of biomass versus time (the derivative approach), the equation can be rearranged

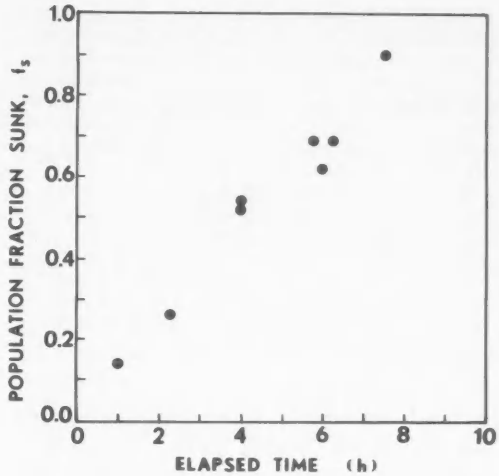


FIG. 3. Linear proportionality between the population fraction settled into the V_s region and elapsed time in eight SETCOL trials. This linearity is in agreement with the underlying theory which calculated the population sinking rate from f_s. The calculated sinking rates were invariant ($P < 0.01$) over the f_s and t ranges described.

$$(9) \quad \psi = f_s \cdot l/t$$

to yield ψ as a function of only the column height, the elapsed time over which settling changed the distribution of biomass, and f_s, the fraction of the original biomass which reached the bottom region V_s during that period. This imparts considerable simplicity to the sinking rate assessment as the only required data are the column dimensions, elapsed time, and the volume and concentration information of the various subsamples.

Discussion — The calibration of values obtained from various sinking rate methods is an important focus of any technique development. Comparison of the values acquired by the SETCOL approach with values based on the direct observation of the arrival rate of cells (e.g. Smayda and Boleyn 1965, 1966a, b) is given in Fig. 4 and shows the mean sinking rate values acquired from the two procedures to be within precision criteria ($P \leq 0.01$) for replicates of either method. The culture conditions of the test populations used in this comparison are identical with those described earlier in connection with Fig. 3. Using another population, a comparison was made between sinking rates acquired by SETCOL and those of the homogeneous sample, fluorometric procedure of Titman (1975) modified by Bienfang et al. (1977). The comparison (Fig. 5) shows that the rate values acquired by the two methods are equivalent ($P < 0.01$). The test population used in this comparison was a NO_3^--limited *D. brightwelli* culture, grown at 16°C under continuous light ($I = 1.5 \times 10^{16}$ quanta·cm^{-1}·s^{-1}). Importantly, these comparisons indicate that sinking rate values acquired via SETCOL analysis correspond to those given by other procedures.

An inherent requirement of the SETCOL method is that

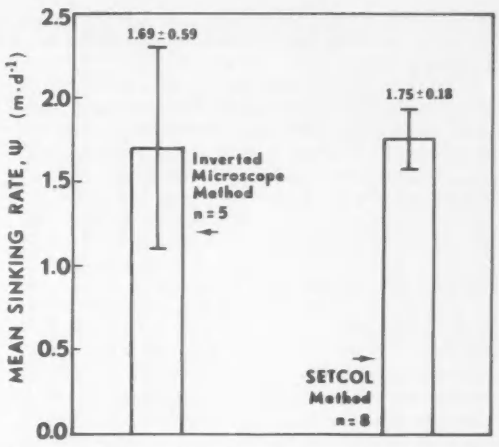


FIG. 4. Comparison of sinking rate values obtained from the SETCOL and inverted microscope methods. These procedures yield equivalent values ($P < 0.01$).

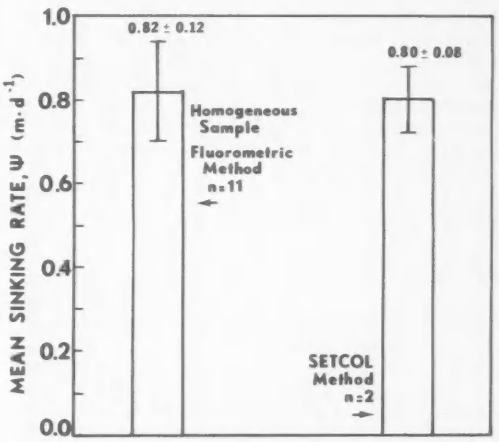


FIG. 5. Comparison of sinking rate values obtained from the SETCOL and homogeneous sample, fluorometric methods. These procedures yield equivalent values ($P < 0.01$).

trials are not run over sufficient duration to allow f_s to attain unity; such occurrence would yield an underestimate of the true sinking rate of the sample. The validity of having met the criterion is easily evaluated in the analysis, and experience with a fair (e.g. >20) number of species having a wide range of sinking rates has shown that this requirement is easily attainable.

Hydrostatic column conditions have been shown by dye studies to be easily obtainable by surrounding the columns in a water jacket circulated by a thermostatically controlled water bath. Observation of neutral density particles and dye studies have shown a decline of initial turbulence (from sam-

ple introduction) within a time (e.g. <10 min) that is short with respect to the typical period of a measurement (e.g. several hours).

To determine if experimental artifacts such as adherence of biomass to the column walls would influence the analytical result, paired sinking rate analyses were conducted in columns having a wide range of surface area to volume (SA:V) ratios. Results showed that the calculated sinking rates were similar ($P < 0.01$) for all cases and independent of the SA:V ratios which ranged over a factor of 9. This result indicates that over the duration of the trial, the availability of surface area does not influence measurement of the rate of passive sinking of the contained sample.

It is often the case that the positively buoyant population fraction and the rate of initial ascent are small in comparison to the negatively buoyant terms. The correction term applied to the positively buoyant subsample (Fig. 2B) accounts for the reality that only the amount of biomass originally present in the short (l_b), upper V_b region can sink out. The response of positive buoyancy has been observed to change markedly in several species following changes in the nutrient regime. Modifications in positive buoyancy concomitant with changes in sinking under fluctuating growth conditions may have considerable ramifications to both description of net losses from a system and to understanding the role of positive buoyancy in providing reinoculation to overlying waters. A significant attribute of the SETCOL approach is the ability to examine the dynamics of positive buoyancy simultaneously with those of negative buoyancy.

The replicability of SETCOL trials is quite good; the coefficient of variation ($SD/\bar{\psi}$) of replicate trials is usually <10%.

The SETCOL approach is extremely versatile and amenable to analyses of a broad spectrum of conditions and/or parameters. Because actual monitoring of the change rate of biomass with time (i.e. the derivative approach) is not required, the experimental environment within the columns is easily manipulable within large limits to provide any range of temperature or photic conditions. The procedure also circumvents most sample handling prior to analysis; test samples are simply added to the columns. The method does not require sample layering inherent to the various discrete sample layer methods (e.g. Smayda and Boleyn 1965; Eppley et al. 1967; Bienfang 1979), and the absence of a need for hyperpycnic column fluid makes the procedure amenable to use with freshwater or seawater samples.

A particularly attractive attribute of the SETCOL approach is that the index of biomass is optional. The biomass index can be selected to focus on various parameters of interest (e.g. carbon, nitrogen, silica, phosphorus, chlorophyll, pheopigment) simply by assessment of the biomass concentration variables ($b_{o,o}$, $b_{o,t}$, b_s, b_b) in those terms. In this way it is possible, for example, to measure the sinking rate of particulate carbon and compare it with that of chlorophyll. Such data may be very informative in the evaluation of changes in the flux of various cellular constituents under different growth conditions. The acquisition of sinking rate terms, ψ, together with standing stock data (e.g. $b_{o,o}$ and $b_{o,t}$) also facilitates derivation of flux terms for the parameters under inspection. The absence of an inherent requirement for viability in the particulate material (e.g. fluorescence or ^{14}C-uptake capability) also means that the procedure can be adapted for the analysis of various types of inert particulate material, e.g. coccoliths, dead cells, sedimentary material.

The procedure has been applied with success to both in vitro cultures and natural subtropical assemblages. Results from oligotrophic coastal waters have shown that the sinking rate of pigmented material was roughly $\frac{1}{10}$ that of total particulate carbon. Such observations reflect the proportions of phytoplanktonic and detrital matter to the pool of total particulate matter in the water column, and exemplify the type of information about vertical transport rates and fluxes attainable by this approach.

ANDERSON, L., AND B. SWEENEY. 1977. Diel changes in the sedimentation characteristics of *Ditylum brightwelli*, a marine centric diatom: changes in cellular lipid and effects of respiratory inhibitors and ion-transport modifiers. Limnol. Oceanogr. 22: 539–552.

1978. Role of inorganic ions in controlling sedimentation rate of a marine centric diatom *Ditylum brightwelli*. J. Phycol. 14: 204–214.

BIENFANG, P. 1979. A new phytoplankton sinking rate method suitable for field use. Deep-Sea Res. 26/6A: 719–729.

BIENFANG, P. K. 1980. Phytoplankton sinking rates in oligotrophic waters off Hawaii. Mar. Biol. 61: 69–77.

BIENFANG, P., E. LAWS, AND W. JOHNSON. 1977. Phytoplankton sinking rate determination: technical and theoretical aspects, an improved methodology. J. Exp. Mar. Biol. Ecol. 30: 283–300.

EPPLEY, R. W., R. W. HOLMES, AND J. D. H. STRICKLAND. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. J. Exp. Mar. Biol. Ecol. 1: 191–208.

LÄNNERGREN, C. 1979. Buoyancy of natural populations of marine phytoplankton. Mar. Biol. 54: 1–10.

ROTHWELL, G. N., AND P. K. BIENFANG. 1978. MARS — a new instrument for measuring phytoplankton sinking rate. Mar. Technol. Soc. J. 12: 13–17.

SMAYDA, T. J. 1970. The suspension and sinking of phytoplankton in the sea. Oceanog. Mar. Biol. Ann. Rev. 8: 353–414.

SMAYDA, T. J., AND B. J. BOLEYN. 1965. Experimental observations on the flotation of marine diatoms. I. *Thalassiosira* c.f. *nana*, *Thalassiosira notula* and *Nitzschia seriata*. Limnol. Oceanogr. 10: 449–509.

1966a. Experimental observations on the flotation of marine diatoms. II. *Skeletonema costatum* and *Rhizosolenia setigera*. Limnol. Oceanogr. 11: 18–34.

SMAYDA, T. J., AND B. J. BOLEYN. 1966b. Experimental observations on the flotation of marine diatoms. III. *Bacteriastrum hyalinum* and *Chaetoceros landeri*. Limnol. Oceanogr. 11: 35–43.

STEELE, J. H., AND C. S. YENTSCH. 1960. The vertical distribution of chlorophyll. J. Mar. Biol. Assoc. U.K. 39: 217–226.

TITMAN, D. 1975. A fluorometric technique for measuring sinking rates of fresh water phytoplankton. Limnol. Oceanogr. 20: 869–875.

Comment on Cycles in the Northern California Dungeness Crab Population

COMMENT

On the basis of a disparity between the period of cycles produced by a model that includes cannibalism and the period of cycles observed in the catch record, McKelvey et al. (1980) claimed that cannibalism on juveniles is not a significant factor in northern California Dungeness crab population dynamics. Knowledge of this disparity is not new (Botsford and Wickham 1978), and it is not a firm basis for rejection of the cannibalism hypothesis. I present here an alternative to their interpretation of the available evidence.

Ricker (1954) demonstrated through simulation that cyclic fluctuations caused by a density-dependent stock–recruitment relationship were roughly of period twice the mean age of reproduction. Since then, Lee (1974), Frauenthal (1975), Allen and Basasibwaki (1974), Botsford and Wickham (1978, 1979), and Levin (1981) have obtained similar results with similar models (i.e. that the period of the cycles is roughly twice the mean lag between the age at which the inter-age, density-dependent effect acts upon younger animals and the age at which older animals cause this effect in younger animals). In particular, Botsford and Wickham (1978), in their study of the same species that McKelvey et al. (1980) studied, noted that a model based on currently accepted life history parameters and cannibalism as an inter-age, density-dependent mechanism, produced cycles whose period was much lower than that observed in the catch data from the fishery. Periods computed by them were as low as 5.75 years (Botsford and Wickham 1978, table 1).

The model of McKelvey et al. (1980) includes both a nonlinear dependence of survival at age zero on older animals and a nonlinear dependence of survival at age one on older animals. They showed that simulations with the latter present produce cycles whose period is lower than the period of cycles in the observed catch record. Up to this point their results are commensurate with those obtained earlier by others. On the basis of this result, however, McKelvey et al. (1980) went on to conclude that cannibalism, as reflected in a nonlinear dependence of survival at age one on older animals, could not be the cause of cycles in the northern California Dungeness crab fishery.

Their method of rejection of the cannibalism hypothesis was a "diagnostic procedure" that they developed. This procedure has two parts. The first part is to formulate a model based on a set of assumptions, derive or compute the resulting behavior of the model, and then compare this behavior to observed behavior of the real system. The second part is to formulate the structure of several different models, fit the parameter values in them to observed population data, and then compare the fit of the different models.

In the first part they formulated a model involving many assumptions, only one of which was the presence of cannibalism. From the fact that behavior of this model does not match observed catch data (i.e. the period is too low), they concluded that cannibalism is not the cause of the cycles. The problem with this conclusion can be cast in both logical and biological terms. In terms of logic they have essentially denied the consequence of a propositional statement. From this one can conclude that at least one of the premises composing the antecedent is false (i.e. one of the assumptions on which the model is based is false). One cannot tell which one. In biological terms, there are many assumptions involved in the model that may not be true. Neither the life history parameters nor the effects of environmental variables are well known. Any change in these elements of the model that changed the delay between the age at which crabs are cannibalized and the age at which they are cannibals would change the period of cycles produced by the model. There is no more reason to conclude that the cannibalism assumption is in error than there is to conclude that assumed life history parameters and effects of the environment are in error.

In the application of the second part of their procedure they formulated several models, one of which included cannibalism. They then showed that models that do not include cannibalism provide a better fit to the data. On this basis they again rejected the cannibalism hypothesis. The problem with this part of the procedure is that it does not provide an independent test of the hypothesis. The primary discriminating factor in both the first and second part of their procedures is the time lag, not necessarily the mechanism. If the model with a "cannibalism lag" doesn't produce cycles of the observed period and models with a "natality lag" do (as shown in part one), then it is obviously true that a model with a "cannibalism lag" will provide a poorer fit to the observed data than a model with a "natality lag". Application of the second part of their procedure is thus a repeat of the first part with the same inherent logical difficulties.

Thus, neither of the two parts of the procedure provides a sound basis for rejection of the cannibalism hypothesis. Their diagnostic procedure suffers from the drawback of allowing rejection of hypotheses which are actually true, simply because one of the model assumptions is not true. McKelvey et al. (1981) state that the diagnostic test on which their conclusion is based "may be legitimately criticized and, in general, diagnostic tests may not be available which might allow the process of elimination approach employed in this study." It seems that the hypothetico-deductive method of science as discussed, for example, in Salmon (1973), would be appropriate and useful here. When following this method, a negative outcome of a comparison of model output to observed behavior would lead to examination of auxilliary hypotheses (e.g. initial conditions, assumptions, etc.) rather than immediate rejection of the hypothesis of primary interest (Salmon 1973). This would avoid the drawback of the diagnostic method of McKelvey et al. (1981).

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Finally, I would like to thank Drs McKelvey and Hankin for inviting me to discuss my work in their seminars at Humboldt State University in early 1978 and for the stimulating discussions that have ensued. — LOUIS W. BOTSFORD, *Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA.*

ALLEN, R. L., AND P. BASASIBWAKI. 1974. Properties of age structure models for fish populations. J. Fish. Res. Board Can. 31: 1119–1125.

BOTSFORD, L. W., AND D. E. WICKHAM. 1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833–843.

1979. Population cycles caused by inter-age, density-dependent mortality in young fish and crustaceans, p. 73–82. *In* E. Naylor and R. G. Hartnoll [ed.] Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford.

FRAUENTHAL, J. C. 1975. A dynamic model for human population growth. Theor. Popul. Biol. 8: 64–73.

LEE, R. 1974. The formal dynamics of controlled populations and the echo, the boom and the bust. Demography 11: 563–585.

LEVIN, S. 1981. Age structure and stability in multiple-age spawning populations. *In* T. Vincent and J. Skowrouski [ed.] Renewable Resource Management. Lecture Notes in Biomathematics. Vol. 40. Springer Verlag, New York, N.Y. 236 p.

MCKELVEY, R., D. HANKIN, K. YANOSKO, AND C. SNYGG. 1980. Stable cycles in multistage recruitment models: an application to the Northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37: 2323–2345.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

SALMON, N. C. 1973. Logic, 2nd ed. Prentice Hall, NJ. 150 p.

REPLY

Botsford and Wickham's work on Dungeness crab population dynamics has been both imaginative and bold. They were the first to make a case that the regular cycles observed in annual commercial landings might not be environmentally driven, but might instead result from a density-dependent biological feedback mechanism (Botsford and Wickham 1975). They may indeed be right about this. However, there are serious problems with their more elaborate conjecture that the feedback mechanism is adult cannibalism of juveniles and that the natural rythmic pattern thus induced is being destabilized by heavy harvesting of male crabs (Botsford and Wickham 1978). While one cannot say categorically that this hypothesis is false, one can show — as we believe we have (McKelvey et al. 1980) — that other mechanisms are more in accord with observation, and one can propose empirical tests — as we also have done — which ought to permit discrimination between the alternative theories.

There are more difficulties with the cannibalism hypothesis than the one mentioned by Louis Botsford in his comment above. Not only do models of cannibalism predict cycle periods substantially shorter than those observed in nature, but as we point out in McKelvey et al. (1980):

1) There is empirical evidence that, contrary to earlier belief, landings of Dungeness crab over a quarter of a century have been quite responsive to the levels of fishing effort, effort which has fluctuated dramatically and increased overall during that time. Hence, observed exaggeration in later amplitude swings of the landings time series is more likely a reflection of the higher percentage harvest removal during recent years than of any destabilization of the underlying cycle of year-class strength.

2) Under such conditions of increasing harvest pressure over time, *both* extant models that assume juvenile cannibalism — Botsford and Wickham's *and* ours — predict that the period of landings should be decreasing over time. No such effect is apparent in the landings time-series.

3) An alternative assumption is of egg or larval stage feedback effects, dependent on density of adult *female* crabs (or, by proxy, the stock's egg capacity). In contrast to the difficulties with the cannibalism assumption, a model of egg–larval feedback combined with actual effort data yields a simulated landings time series quite compatible with the historical record. There is no difficulty in matching the observed constant period of cycling nor, for the most part, the increasing amplitude of swings of catch in recent years.

In his comment, Dr Botsford argues that both our model of cannibalism and our means of analyzing it are flawed. The principal structural difference between our model and his is in a different explicit time lag for the feedback (apparent in the renewal equation formulations.) This affects the period of cycling but does not bear on the other difficulties cited above. Regarding the explicit time lag, we believe that the Botsford — Wickham model contains a structural error which is obvious when the model is derived in a more fundamental way (essentially via a Leslie matrix). However, Dr Botsford is correct in emphasizing the importance of the model's *effective* time lag, involving an appropriate population average of adult ages: "Any change in these elements of the model that changed the delay between the age at which crabs are cannibalized and the age at which they are cannibals would change the period of cycles produced by the model." Among these elements, he specifically cites "assumed life history parameters and effects of the environment."

The assumptions in our models which bear on the effective delay include:

a) The unexploited survival rates for adult males and adult females.
b) The level of exploitation in the fishery.
c) The vital life history parameters of female crabs, including size at age and longevity (which we take to be 6 years).

As recorded in McKelvey et al. (1980), a careful sensitivity analysis shows that our model's behavior is quite robust with respect to the first two listed assumptions. In particular, neither model of cannibalism, if formulated with correct explicit time lag, can be brought by parameter adjustment into conformity with the historical landings record. However, the period of cycles generated by the alternative density-dependent egg–larval recruitment mechanism does depend sensitively on assumptions made concerning female crab growth and, in particular, maximum reproductive age. In this way our modeling exercise has pinpointed the need for some specific empirical work.

Following up on this, one of us (DGH) proposed and had

funded a California Sea Grant research project to determine the vital life history features of the female Dungeness crab in northern California. Preliminary results from the 1st year of the study, presuming they are supported by further data collection, show remarkable (almost embarassing) agreement with our modeling assumptions. To our surprise, the size of molt increments have been roughly independent of initial female size and have generally fallen between 12- and 15-mm carapace width. Given that the average size of a female at age 2 is about 115 mm (Poole 1967), and applying the above increments, gives a size of about 175 mm at age 6 or 7. None of the more than 6000 females collected have exceeded 170-mm carapace width, although there have been very strong numbers in the high 150's. Likewise, annual California Dep. of Fish & Game cruises since the midfifties indicate that a female crab in excess of 170 mm is an extreme rarity (R. Warner, CDFG, personal communication). In addition, it has been extremely rare to find females exceeding 155 mm in premating embraces, a fact which is also often stated by local fishermen. If female crabs molt once each season, it seems quite likely that 6 or 7 years is, in fact, maximum longevity in northern California.

We want to stress that we are in no way claiming to have "proved the validity" of the egg–larval feedback mechanism, though we believe that we have cast very serious doubt on the validity of currently proposed models based on cannibalism. "There is always something about the real world which an abstract model will fail to predict, and there is always some model which can be constructed to mimic a given portion of real world behavior. Proper validation is not a matching game, but rather an effort to explore the limits of model credibility. The establishment of these limits requires invalidation, not validation . . . A minimum requirement is agreement with a range of observed temporal and spatial patterns under a wide variety of extreme conditions" (Clark et al. 1979).

Agreement with historical patterns is thus necessary to avoid invalidation, even though agreement is far from sufficient for validation. But "a wide range of extreme conditions" may be hard to come by in nature. This explains the two-part structure of our diagnostic procedure: our one approach, the more traditional, is to try to fit a model to the historical time series of landings. Our other approach is to examine simultaneously several models incorporating different assumptions and, through mathematical analysis and simulation, to compare their behaviors under a variety of real *or theoretically conceivable* conditions.

Thus, for example, we use the models to predict the effect of initiating a female harvest. (The commercial fishery historically has taken only males.) Assuming the egg–larval mechanism, we find that the average population level should increase and the amplitude of cycling should be damped. Dr Terry Butler (Pac. Biol. Station, Nanaimo, B.C., personal communication) has suggested that such a real experiment might indeed be possible on certain isolated west coast stocks of Dungeness.

We have also had an opportunity, since the publication of the paper, to test our egg–larval model against a real-world extreme: the catastrophic decline in the late 1960's of the Central California crab fishery. Wild (1981) has established a strong statistical correlation between this decline and a sudden shift upwards in water temperatures that occurred over a wide area at that time. The biological link is a laboratory-established strong decrease in egg survival as water temperature rises. If this sudden drop in survival is incorporated into our egg–larval model (via a decrease in a density-independent natality parameter), the model predicts both a substantial decline in population averages and a damping of the cycles — exactly as was observed. Wild's paper also shows that the extremely large year-class which dominated the northern California fishery during 1977 coincided with extremely cool and unusual ocean water temperatures during the cohort's egg/larval stages. Hence the recent "wild" amplitude swing may merely reflect unusually good survival conditions.

Our point has not been to seek an illusory ultimate verification of any particular model, but to illustrate a modeling process: an iterative procedure whereby each stage of modeling triggers empirical investigation which then permits building a next generation model. We also wished to illustrate the rewards of plunging into model construction even at an early stage of knowledge, when quantitative data may have been sketchy or lacking. In fact, a modeling exercise can help determine which data are most critical to obtain, and may also suggest the most appropriate level of detail for which to aim.

A comment by a reviewer of our original manuscript seems apropos: "The criticism that every potential factor is not included in the modeling to arrive at the conclusion is valid — and self-defeating. Obviously there may always be more factors yet undiscovered, implying by this logic . . . that the issue can never be resolved. In times of depression one might agree with this nihilism, but fisheries is a practical art and not a science. We must look for a rational explanation of observed phenomena." — ROBERT MCKELVEY, *Mathematics Department, University of Montana, Missoula, MT 59812, USA* AND DAVID HANKIN, *Department of Fisheries, Humboldt State University, Arcata, CA 95521, USA*.

BOTSFORD, L. W., AND D. E. WICKHAM. 1975. Correlation of upwelling index and the Dungeness crab catch. Fish. Bull. 73: 901–907.

1978. Behavior of age-specific density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833–843.

CLARK, W. C., D. D. JONES, AND C. S. HOLLING. 1979. Lessons for ecological policy design: a case study of ecosystem management. Ecol. Model. 7: 1–53.

MCKELVEY, R., D. G. HANKIN, K. YANOSKO, AND C. SNYGG. 1980. Stable cycles in multistage recruitment models: an application to the Northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37: 2323–2345.

POOLE, R. L. 1967. Preliminary results of the age and growth study of the market crab (*cancer magister*) in California: the age and growth of cancer magister in Bodega Bay. *In* Proc. Symp. on Crustacea, Part II. Mar. Biol. Assoc. India. 553–567.

WILD, P. W. 1980. Effects of Seawater temperature on spawning, egg development, hatching success, and population fluctuations of the Dungeness crab, *Cancer magister*. Cal. COFI Rep. 21: 115–120.

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Advantages of Eigenvectors Over Structure Coefficients as Indicators for Selecting the Response Variables in Principal Components

COMMENT

Principal component analysis (PCA) is a popular statistical tool among biologists (e.g. Green 1971; Gauch and Whittaker 1972; Orloci 1975). It is often used to examine the relationship between species associations and physical and chemical conditions in an environment. This method is a general transformation technique which effectively uses ordination to reduce data dimensionality while sacrificing little information.

Sprules (1977) and Sprules and Holtby (1979) used this method on the zooplankton species abundance data by transforming the original information matrix of lakes by species to one of lakes by principal components, where principal components (Y_j) are linear compounds of the original variable (X_i). After computing the rank correlations between the first two principal components and six selected environmental variables, Sprules (1977) was able to demonstrate that different limnological conditions of lakes can be indicated by the crustacean zooplankton communities they support. Before this, he used structure coefficients (the product–moment correlation coefficients) between the variables (X_i) and principal components (Y_j) to show the relative importance of original variables (X_i) to the principal components (Y_j). This application touches upon the important question of whether eigenvectors (loading coefficients) or structure coefficients (product–moment correlation coefficients) are a better index for the relative importance of the original variables (X_i) in the principal components when the selection of principal components has already been made.

The argument for using structure coefficients is that eigenvectors (loading coefficients) indicate only the direct contribution of the original variables to the calculation of the principal components. Since the effects of correlations among variables (X_i) and the resultant indirect contributions may not be immediately apparent, the use of structure coefficients is a way to present all the contributions from the original variables (X_i) to the principal component (Y_i). Sprules (1977) and Sprules and Holtby (1979) used this method by selecting those species or groups which showed a significant structure coefficient with the principle components. Sprules explained (1977) that rare and common species alike can have a high correlation with a component so long as their abundance varies greatly over the lakes. However, the result was that species or groups having little direct contribution to the components were included in the list of important contributors to the components. Such use represents an inflated estimate of the relative contribution to the principal component by original variables having an eigenvalue greater than 1.

The disadvantage of using structure coefficients may be illustrated as follows. The reason for using PCA is the multivariate collinearity of the data. Such collinearity between the variables is difficult to separate, but if this is used, the dimensionality can be sufficiently reduced. PCA takes advantage of such collinearity to accomplish its data reduction. Therefore, it is fair to assume that a strong collinearity is the basis for a successful application of PCA. However, when a structure coefficient is computed from data exhibiting collinearity, it involves not only the direct correlation between the variable X_i and component Y_j, but also the indirect correlation between them via other variables. This presents no problem if only one structure coefficient is computed for variables (X_i) and component (Y_j), but to estimate the relative importance of the original variables (X_i), all structure coefficients have to be calculated between the original variables (X_i) and the component (Y_j). Nonetheless, if more than one structure coefficient is computed, the collinearity is undoubtedly being considered more than once. Such repeated use of the collinearity estimates thus produces an inflated contribution from original variables to the principal component. This in part can be seen in cases in which the higher the correlation between the variables (X_i) is the greater the variance (eigenvalue) of the first principal component, since the eigenvalue is the sum of the squared structure coefficients. The effect of this overestimate is that relatively unimportant variables show a significant contribution to the principal component.

This can also be examined from a numerical point of view. The structure coefficient (product–moment correlation coefficients) of the ith variable and the jth component is $\alpha_{ij}\sqrt{\ell_j}/S_i$, where α_{ij} is the eigenvector (loading coefficients), ℓ_j is the eigenvalue of the component, and S_i is the standard deviation of variable X_i. If the component is extracted from the correlation matrix, the structure coefficient of the variable X_i with the jth component is simply given by $\alpha_{ij}\sqrt{\ell_j}$. Therefore, the structure coefficients show not the relative importance of variables to the component, but the product of the relative contribution of the variable to the component with the square root of the variance (eigenvalue). Since the principal components are determined prior to the selection of relatively important variables for each component, it is reasonable to consider only eigenvectors (loading coefficients) for evaluating the contribution of the original variables to a principal component. The point is made amply clear in Afifi and Azen (1973) that to compare the contribution of variables $X_1 \ldots X_p$ to principal component Y_j based on covariance matrix, one should examine the quantities α_{ij}/S_i, $i = 1, \ldots p$. When the correlation matrix is used, the comparison of the coefficient α_{ij} is all that is necessary. While the principal component is not selected prior to the evaluation of the original variables, I feel that the structure coefficients may be used to select those components which correlate highly with the original variables — WILLIAM Y. B. CHANG, *Great Lakes Research Division, The University of Michigan, Ann Arbor, MI 48109, USA.*

AFIFI, A. A., AND S. P. AZEN. 1973. Statistical analysis: a computer oriented approach. Academic Press, Inc., London. 366 p.

GAUCH, H. G. JR., AND R. H. WHITTAKER. 1972. Comparison of ordination techniques. Ecology 53: 868–875.

GREEN, R. H. 1971. A multivariate statistical approach to the Hutchinsonian Niche: bivalve Molluscs of central Canada. Ecology

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52: 543–556.
ORLOCI, L. 1975. Multivariate analysis in vegetation research. W. Junk, the Hague.
SPRULES, W. G. 1977. Crustacean zooplankton communities as indicators of limnological conditions; an approach using principal component analysis. J. Fish. Res. Board Can. 34: 962–975.
SPRULES, W. G., AND L. B. HOLTBY. 1979. Body size and feeding ecology as alternatives to taxonomy for the study of limnetic zooplankton community structure. J. Fish. Res. Board Can. 36: 1354–1363.

REPLY

Principal component analysis (PCA) is merely a mathematical tool for reducing the dimensionality of multivariate data. Biological interpretation of the data structure revealed by PCA is the most important task of the ecologist. Chang appears to recommend that I should have used eigenvector elements (loading coefficients) rather than product–moment correlations between species and components, to interpret species patterns summarized by the PCA (Sprules 1977; Sprules and Holtby 1979). In this he is incorrect as the following will show. Although my comments apply to covariance matrices, they are equally applicable, with slight modification, to correlation matrices.

Since the principal components I computed from the zooplankton species variance–covariance matrix are new derived variates, each will have a value for every lake in the original data set. This value, or score, of the *j*th component for a particular lake is given by

$$Y_j = \alpha_{1j}X_1 + \alpha_{2j}X_2 + \ldots + \alpha_{nj}X_n$$

where the α's (elements of the *j*th eigenvector or Chang's loading coefficients) are weightings indicating the contribution of each species to the component score, and the X's are the raw abundances for each of the n species (variates) in that lake. Ordination of these scores is the basis for assessing interrelations among lakes in terms of their zooplankton associations. The loading coefficients per se are used only in the calculation of these scores (Cooley and Lohnes 1971; Morrison 1976).

Chang confuses this stage of PCA with the next, namely the interpretation of the species patterns summarized by the principal components. An analogy with linear regression analysis will help to differentiate these two stages in PCA. In a simple case, the value of a dependent variate, W, could be determined by the level of an independent variate, T, according to

$$W = bT + a$$

where b is the regression coefficient of T on W and a is the intercept. The coefficient b simply gives the weighting of T in the prediction of Y (analogous to the computation of component scores). To assess whether b differs significantly from zero, i.e. whether T "explains" a significant portion of the variance in W (analogous to interpretation of principal components), a statistical assessment (e.g. ANOVA) is made. Clearly the numerical value alone of the parameter b is an insufficient basis upon which to gauge the importance of T. The significance of any parameter estimated from a random sample must be assessed in relation to its standard error.

Similarly, in my analysis of zooplankton species, the eigenvector elements alone are not sufficient to assess the importance of the individual species to a component. A statistical evaluation is required which, in the case of PCA, involves the product–moment correlation between the *j*th component and the *i*th species. It is the examination of these correlations which "... is the primary interpretive device in principal components analysis .." (Cooley and Lohnes 1971). This examination determines which species make statistically significant contributions to the components and thus reveals the underlying patterns of species associations in the lakes. Some species in my studies had comparatively low loading coefficients and hence made little contribution to *the calculation of component scores of lakes* (mainly because these species were never abundant), but they nevertheless showed variations in abundance over the lakes which were *significantly correlated with some components*. Had I based my interpretation only on eigenvector elements, as Chang proposes, I would have underestimated the importance of some species.

Chang's concluding paragraph makes confusing recommendations. Having proposed eigenvector elements (α_{ij}) for evaluation of variates, he then recommends α_{ij}/S_i (S_i is the standard deviation of the *i*th variate), citing Afifi and Azen (1973). This quantity differs from the correlation between the *i*th variate and *j*th component only through multiplication by the constant $\sqrt{\ell_j}$ (ℓ_j is the eigenvalue of the *j*th component). There is thus nothing whatever to be gained by using α_{ij}/S_i in preference to the correlation coefficient. Although Afifi and Azen (1979) do recommend this unusual quantity on page 322, they in fact employ correlation coefficients for interpreting underlying data structure in a worked example which immediately follows. Surprisingly, Chang's final recommendation is for the use of structure coefficients, i.e. correlations! His qualifications in this paragraph relating to the determination of components prior to the selection of important variates are irrelevant. Components are calculated, typically by computer, after which the biologist assesses the importance of variates by examining their correlations with components.

Some comment on Chang's treatment of collinearity and associated redundancies of component correlations with species is required. His comments about direct and indirect contributions of variates to components are incorrect, as the following will show. If one begins with a correlation matrix among variates, then all variances are unity, for this is an implicit scaling effect of computing correlations. The total variance in the data set is the sum of these unit variances, or equivalently the number of variates. On the basis of pattern in variances and correlations in this matrix, principal components are extracted, each having a unique variance or eigenvalue. The sum of these component variances is equal to the total variance of the original data set. Thus the original variance is simply reapportioned among components. The variance of each component is equal to the sum of its squared correlations with the variates; the total variance of each variate is the sum of its squared correlations with all components. The original variance, thus parsimoniously redistributed among the components, can be completely recovered from the

principal components solution. The correlations of variates with components do not create redundancies, as claimed by Chang, but simply summarize a new organization of the original variance. It follows that high variate correlations with the first component are indicative of a very efficient solution, for most of the original variance is contained in this one component. There is no overestimation of variate contributions, again as claimed by Chang.

Other confusing phrases such as "... variables having eigenvalues greater than 1" undermine much of what Chang has to say. The fact is that the only rigorous procedure for interpreting the importance of variates in principal component analysis, whether based on a covariance or correlation matrix, is to examine the pattern of correlations between components and variates. There are many difficulties with PCA when it is applied to ecological data (Green 1979), but these include none of the points mentioned by Chang. — W. G. SPRULES, *Department of Zoology, University of Toronto, Erindale College, Mississauga, Ont. L5L 1C6.*

AFIFI, A. A., AND S. P. AZEN. 1973. Statistical analysis: a computer oriented approach. Academic Press, Inc., London. 366 p.

1979. Statistical analysis: a computer oriented approach. (2nd ed.). Academic Press, Inc., London. 442 p.

COOLEY, W. W., AND P. R. LOHNES. 1971. Multivariate data analysis. John Wiley & Sons, Inc., New York. 364 p.

GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons, Inc., New York. 257 p.

MORRISON, D. F. 1976. Multivariate statistical methods (2nd ed.). McGraw-Hill, Inc., New York. 415 p.

SPRULES, W. G. 1977. Crustacean zooplankton communities as indicators of limnological conditions; an approach using principal component analysis. J. Fish. Res. Board Can. 34: 962–975.

SPRULES, W. G., AND L. B. HOLTBY. 1979. Body size and feeding ecology as alternatives to taxonomy for the study of limnetic zooplankton community structure. J. Fish. Res. Board Can. 36: 1354–1363.

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BOOK REVIEWS/COMPTES RENDUS

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Charrs, Salmonid Fishes of the Genus *Salvelinus*. *Edited by Eugene K. Balon. Dr. W. Junk BV Publishers, The Hague, The Netherlands. 1980. ix + 928 p. $250.00*

This book is the first in a series of monographs which the editor, Dr Eugene Balon, of the University of Guelph, Ont., intends to carry on, if for no other reason than to "find a dignified home" for his major research program. Because this books is authored by so many prestigious experts, a total of 40, on a subject important from both scientific and economic viewpoints, because it is the beginning of a major series, and certainly because of its outrageous price (in excess of $250.00 Canadian, direct from the publisher), it demands close examination.

At that price, it is nearly 10 times more expensive than most books its size. For those willing to flaunt the copyright laws with a photocopying machine, it could be copied for about one-quarter its selling price (Junk is famous for overpriced reprints of very old, valuable, reference works which are otherwise not obtainable). Reprints were made available to the authors, who have been generous in passing them on to interested students of chars.[1]

As far as I have been able to determine, the cost is not the result of having had to pay the authors. Does the book have the technical quality to justify the high price? Definitely not. The paper and type are reasonable, but not superb. The copy editing is flawed. The line drawings, evidently supplied by the authors, are of various styles, labeled with different types, and often of an awkward shape, resulting in a number of excessively small figures which nearly require a magnifying glass to read. In some cases, the figures are unnecessarily large (including some very simple line drawings of developing embryos). For an expensive book, the reproduction of the photographs is very poor. Although a simple three-color separation process, the colors were out of register in each of the three copies I checked. In many cases, I could not see the point of the color photographs. The black and white figure of the lake, brook, and splake chars in Berst et al. is superior to the color frontispiece, primarily because the authors chose a better set of examples. The photographs of cleared and stained alevins were less informative than line drawings would have been. While good photographs are certainly preferable to paintings of drawings of specimens for showing color markings and even pigment patterns, many of the black and white photographs in this book are bad enough that it is difficult to acknowledge their usefulness. Thus, the high price cannot be due to a lavish format and production. Perhaps the print run was made to equal exactly the number of char experts plus rich libraries, guessing that the whole run would sell even at an exorbitant price to those who 'must' have it.

The preface is in three parts, the first by the editor. Then a two and a half page amusing not on spelling (char, charr, or charre) ends with a plea that editors allow authors to spell the word as they see fit. I presume the editors ignored this plea, because I find it hard to believe that all 40 authors would have prefered "charr," which is used slavishly throughout. Finally, a token note on the use and harvest of char by the Arviligjuarmiut (one of the Inuit groups) concludes with the information that the char is half of their diet, presumably a plea for the preservation of char.

An epilogue by Regier echoes this sentiment on a broader base, recommending the establishment of a "charr watch" which would be a "Network of informed scientists together with dedicated environmentalists, naturalists and anglers ... that would seek to produce comprehensive periodic reports on the status of charr across the hemisphere. In this way, charr could serve a role as a miner's canary ... to warn of impending or ongoing destruction for vast areas of northern biomes." As with many of Regier's summary articles, it is somewhat tongue-in-cheek. His serious call for a synthesis, however, is partly answered by the book.

Some very thick and juicy slices of meat are to be found in this sandwich of information on chars. The book begins with a review of the four main chars based on the literature, and in some cases on the current work of the author. Each chapter attempts to cover distribution, stocks, reproduction, life history, ecology and 'population dynamics.' The latter is distinguished from the ecology of the beasts by the economic applicability. These four chapters form a platform from which the rest of the book can be profitably digested, even if the reader is a complete novice in the field. The least weight of information is found in the chapter on the Dolly Varden (*Salvelinus malma*), reflecting both the relative inaccessibility of this fish and its somewhat limited economic importance.

The second section of the book deals with the taxonomy, biogeography, phylogeny, and morphology of chars, and contains a fascinating argument about the mechanism of speciation in the chars, and to what degree this speciation has occurred. Three approaches to solving the most difficult problem, i.e. the specific status of *S. alpinus* (Arctic char) vs. *S. malma*, are used by several different authors, and many of the other authors speculate on the possibility of two distinct methods of 'evolution' having occurred with the chars. Morrow uses multivariate techniques of discrimination based on phenetics, and concludes *S. alpinus* and *S. malma* are distinct species with two 'forms' of the Dolly Varden (a northern and a southern). Cavender, in an exhaustive analysis of certain osteological and meristic characters concludes that there are at least seven and possibly nine fully differentiated

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[1]The *Canadian Journal of Fisheries and Aquatic Sciences* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (4th ed. 1980), Spec. Publ. No. 12, Am. Fish. Soc.

species in the genus *Salvelinus*, four 'forms' of *S. malma* (north, south, east, and west), and two or three additional species in the *S. alpinus* complex. Mednikov, Maksimov, and Savvaitova conclude on the basis of an analysis of genetic divergence that *S. alpinus*, *S. malma*, and all their 'forms' are the same species. Behnke recognizes *S. malma*, *S. alpinus*, *S. confluentus*, and *S. profundus* in this complex and discusses several "tentative" species. As well, he names numerous subspecies. Non-taxonomists, take your pick!

The fundamental disagreements are based on the underlying concepts of evolutionary mechanisms. Savvaitova argues that while it is possible to classify the chars on the basis of combinations of key characters, the taxonomic rank of these distinctions is unclear. Further, because there are homologous though geographically remote forms, a dilemma is created if they are recognized as species. She concludes it is possible to have parallel variability (=evolutionary convergence?) on a grand scale, explaining the mosaic geographic distribution of these apparently homologous forms. Because of the abundant examples of forms that have different ecological habits and sometimes different spawning times occurring in the same body of water, she concludes that there may have been a sympatric origin of taxa based on a polymorphism in the populations. Such polymorphic origin seems to have occurred only in freshwater forms of char, a fact which is consistent with a theory that recessive phenotypic characters are expressed at the boundaries of a species' distribution. Thus, on transition to freshwater in small ancestral populations, homozygotes of recessive characters adapted to the given conditions are eliminated, giving rise to apparently the same form independently. Other explanations of speciation in this group based on geographic separations, according to her, require paleographic speculations that at times sound like science fiction.

In a chapter that appears to be out of place (in the next major section), Klemetsen and Grotnes argue that because the life history and serum esterase allele frequencies are distinct, there is no evidence for sympatric origin of the two forms. They present no hypothesis which would allow separation of species formed by allopatry from those formed in sympatry so the discussion is largely irrelevant and their case is a statement of belief, not supportable theory.

Nearly two hundred pages of the book are given to detailed descriptions of the early ontogeny of *S. namaycush* (lake trout), two subspecies of *S. alpinus* (Sunapee and Arctic char), and *S. fontinalis* (brook trout) by Balon. He draws comparisons among the species, and alludes to the taxonomic problem cited above, noting the existence of altricial and precocial forms of the same taxon in sympatry, but says with a literary shrug of the shoulders, there may not be a speciation process involved. He also declines to provide a key to the early life stages, defending this omission with argument that all recent studies have identification as their ultimate goal, a goal Balon finds too narrow. It is presumably a desire to remain unsullied by such mundane needs tht he is prevented from providing a key based on other than the 'elimination of most other possibilities' puzzle in keys to which he has previously objected.

Considering the scope of this book, it is a disppointment to find so little on the behavior of the chars. Excellent observations on the feeding mechanisms are presented by Lauder and Leim, a paper which has many insightful comments sprinkled through it. Leggett discuses the reproductive behavior of Dolly Varden, and in the paper on splake, the same subject is outlined for the hybrid.

A chapter by MacCrimmon and Gots depicts the decimation of stocks on a worldwide basis, resulting from a combination of factors including overexploitation, which they appear to feel is the dominant cause, except in the case of the lake char, where the decline of water quality and the inadvertent introduction of lampreys to the habitat were equally important.

The last full chapter documents the attempt to 'create a new taxon' and thus combat the depredations of the lamprey. This excellent paper, by Berst, Ihssen, Spangler, Ayles, and Martin, the investigators largely responsible for implementing the program, unfortunately ends on the lame note that the mortality of the hybrid under natural conditions in Lake Huron has been greater than anticipated, and the program appears to be under review. One hopes the future of char is not as dismal as the last two chapters suggest might be the case.

Should you buy the book? If salmonids are your game then dig deeply into your shrinking wallet, it probably is a must. If not, then read it in the library.

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(R-322)

Aquatic Microbiology. *G. Rheinheimer. John Wiley & Sons, New York. 1980. 235 p. $28.00 U.S.*

The first German edition of *Aquatic Microbiology* preceded the English translation by Anna Mayr−Harting of 1974 by 3 years. Commendably this second edition and its translation by Norman Walker were both published virtually simultaneously in 1980, with literature references included up to 1979. The book is increased slightly in dimensions and contains 51 more pages and approximately 100 more references. It is printed in the German Democratic Republic and the quality of the photomicrographs is considerably improved over those of the first edition, which suffered from a somewhat excessive contrast.

The book provides a brief, but useful, survey of the microorganisms found in freshwater, salt lake, and marine environments. New sections on the cyanobacteria (here still called the Cyanophyta) and viruses are included. Examples of the distribution of microbial numbers and biomass in different types of aquatic systems, including sediments, are then presented. Not unnaturally, most of the examples discussed are from European and Soviet authors and Dr Rheinheimer draws frequently from his own work on the Elbe and the Kiel area in general. The effect of light, temperature, and many other factors on the activities and distribution of microbes in aquatic systems is well treated, as is the variety of interactions between microorganisms, ranging from competition to parasitism.

The production and decomposition of organic materials as

well as the cycles of C, N, P, S, Fe, and Mn are all covered in 35 pages and the treatment is therefore necessarily somewhat superficial. Food chains and energy flow are introduced for the first time in this second edition, but again, the discussion of the four block diagrams presented (two are from Ellenberg's Ökosystemforschung) is minimal. Microbiology of sediments, mineral resources, water pollution, and finally economic aspects of fermentation spoilage, biodeterioration, and the leaching of ores are topics that complete this wide survey of the broad field of aquatic microbiology. It is not, nor does it set out to be, an in-depth reference source for the specialist in any of the topics covered. However, the book as a whole is a very useful survey and can be recommended for general reading by all those interested in aquatic systems. In the present climate of escalating book costs, it is a good value at this price.

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(R-354)

Fisheries Biology: A study in population dynamics (2nd ed.). *D. H. Cushing. The University of Wisconsin Press, Wisconsin. 1981. xvi + 295 p. $17.00 U.S.*

Properly titled, this book would be called "Fisheries Biology: The View from Lowestoft." It is a fine volume, in the best traditions of the laboratory, building on the major syntheses that have gone before — of Russell, Graham, Beverton and Holt, Harden-Jones, Gulland, the author David Cushing, and several others of the famous United Kingdom center. The book is intended to convey what fisheries biology is all about, and as far as the view from Lowestoft is concerned, it is a first-class job. The author is thoroughly familiar with work in the United Kingdom and the neighboring European countries, and can accordingly present an impressively coherent account of the understanding of the North Sea and North East Atlantic fisheries. In that respect, the book is a model for others to follow in developing comparable appreciations.

It is also a fine introduction for the beginner because it exposes the major elements of the subject in a lucid manner, with an abundance of broad generalizations to keep the reader always aware of the contexts within which the various elements must be considered. Thus, the chapter on migration is tied tightly to the chapter on the idea of a unit stock, and both are brought together in a chapter well titled, "Fish in Space and Time." The chapter on growth is well wedded to the chapter on mortality, and both join up with the chapters on abundance and recruitment in leading to the chapter on models used in management. The book is superbly put together as a logical exposition of the full dimensions of fisheries biology.

It has its faults, of course, which tend to be directly proportional to the distance from Lowestoft to the subject area under discussion. The attention given to the fisheries of the North Pacific is much less than that concerned with the North Atlantic. The tropical fisheries get only occasional passing mention and freshwater fisheries are virtually unmentioned. There is no discussion of recreational fisheries, nor of aquiculture, freshwater or marine. For those who are looking for a comprehensive global coverage of the subject of fisheries biology, the book can only be disappointing. The strength of the presentation lies in its depth and discernment, and in the potential application of scientific principles to fisheries everywhere.

Many of these comments were made at the time of publication of the first edition of this book in 1968, and my own review at that time was quite critical of its narrowness. Wisely, I think, David Cushing chose to make the second edition deeper, more profound, and still essentially Lowestoft oriented, rather than to respond to the criticisms of its parochial flavor.

Unfortunately, in the second edition, there are still several bloopers about Pacific salmon, and there are a few minor errors in some of the mathematical formulations. These are only minor blemishes in a tapestry that is most impressive, but they are quite "off putting" to the reader who is aware of them. Fortunately, none is so serious as to upset the logic of the stream of argument. They are rather reminiscent of badly played golf strokes that nevertheless put the ball in the hole.

Technically speaking, the book is almost ideal for a text. There are 103 figures to make things stick graphically, a list of symbols and their definitions, a glossary, a comprehensive set of references, and a good index.

The essence of the perspective of this fine work, reflecting long experience and considered judgment, is contained in two sentences in the second-to-last chapter. "The needs of management become ever more complex and demanding. The broader the base of fisheries biology, the greater the chance of satisfying those needs." The author has done an exceptional job of describing the base and its relevance. I would recommend it highly to those who aspire to a career in fisheries biology.

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(R-355)

Common Intertidal Invertebrates of the Gulf of California, Second Edition. *Richard C. Brusca. University of Arizona Press. Tucson, Arizona. 1980. 513 p. $26.95 U.S.*

The Gulf of California, an 1100-km rift in the continental margin, protected by the Baja California Peninsula from the chilling effects of cold-water upwelling, is an awkward disturber of neat neritic biogeography. Tropical east Pacific elements are carried far to the north and the special conditions have given rise to a high proportion of endemic taxa.

The Gulf is well known biologically, but this volume is the sole comprehensive treatment of the invertebrate fauna. Though more than 1300 species are treated, it is unfortunate

that only common animals are included, reducing the value of this book to the scientist. It is saved from being the usual lucubration of keys and lists (which are as plentiful as mushrooms after summer rain) by the thoughtful introduction covering the geological evolution and physical regimes of the Gulf of California.

Although this volume is not requisite reading for septentrional workers, it furnishes an attractive overview of a warm-water fauna, and will be especially useful to those of us concerned with identifying transported exotics.

The various groups have been treated by several contributors and some sections have been directly taken, with acknowledgments, from standard published works. A welcome departure is the inclusion of Arachnida and Insecta frequenting the intertidal zone. The diagnostic characters given are concise and keys well supported by the clear line illustrations. Included is the usual quota of color plates that provide only marginal help for identification, but increase the cost of production. It is unfortunate that, for many books aimed at a wider audience, it is almost prescriptive that color plates be included. The best that may be said is that they provide a slight, but not useful, esthetic fomentation, particularly on the rare occasions when the colors are accurate.

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(R-352)

Books received / Livres reçus[1]

May–June / mai–juin 1981

***Integrated Agriculture–Aquaculture Farming Systems.** *Edited by R. S. Pullin and Z. H. Shehadeh. ICLARM (International Center for Living Aquatic Resources Management). Manila, Philippines. 1980. vii + 258 p. ?.* (This soft-cover book is the proceedings of the ICLARM–SEARCA Conference on Integrated Agriculture–Aquaculture Farming Systems, held in Manila, Philippines, August 6–9, 1979.

***Black Cod: Boom or Bust?** *Edited by Charlotte Henry. Washington Sea Grant Publication, Seattle, WA 98105. 1981. vi + 25 p. $1.50 U.S.* (Proceedings of a seminar held in Seattle, Washington, February 27, 1980.)

***Fish Diseases.** *Edited by W. Ahne. Springer-Verlag, New Jersey. 1980. xi + 252 p. $49.80 U.S.* (This book records contributions presented at the Third Session of the EIFAC (European Inland Fisheries Advisory Commission on the Food and Agriculture Organization of the United Nations) and OIE (Office International des Epizooties) Cooperative Programme of Research on Aquaculture (COPRAQ) Fish Diseases. The session was held at the Institute for Zoology and Hydrobiology, Veterinary Faculty, Munich, on October 23–26, 1979.)

The Physiological Ecology of Phytoplankton. *Edited by I. Morris. University of California Press, Los Angeles. 1980. x + 635 p. $74.50 U.S.* (This book is concerned with the way in which phytoplankton growth and distribution is controlled by an interaction between environmental factors and the cellular physiology of the algae.)

***The Estuarine Ecosystem.** *Donald S. McLusky. Halsted Press, John Wiley & Sons, New York. 1981. viii + 150 p. $29.95 U.S.* (This book appears to be aimed at the senior, non-honors, undergraduate; its emphasis on biological productivity and energy flow makes it useful beyond the marine biology student).

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[1]Entries in this list *not* marked by an asterisk are available from review by interested readers for a 3-month period from the time of publication of the list. For information, please write to the book Review Editor.

[1]Les ouvrages inclus dans cette liste et *non* accompagnés d'un astérisque peuvent être mis à la disposition de lecteurs intéressés qui voudraient en faire l'analyse, et ce, pour une période de 3 mois à compter de la date de parution de la liste. Pour plus de renseignements, veuillez écrire au rédacteur des Comptes rendus.

ANNOUNCEMENTS / AVIS

First International Symposium on Off-Flavours in the Aquatic Environment

This Symposium will be held in Espoo, at the outskirts of Helsinki, Finland, on June 14–18, 1982. It is sponsored by the International Association of Limnology and various Finnish national bodies including the Finnish Limnological Society and the Water Association of Finland.

Most aspects of flavor (odor and taste) problems in water and aquatic organisms (psychophysics, chemistry, biology, and technology) will be covered during the symposium.

For further information, please contact one of the following: *Dr Taina Kuusi, Secretary of the Symposium, State Technical Research Centre, Food Laboratory, Biologinkuja 1, SF-02150, Espoo 15, Finland;* or *Dr Per-Edvin Persson, Chairman of the Program Committee, University of Helsinki, Department of Limnology, Viikki, SF-00710 Helsinki 71, Finland.*

Premier colloque international sur les saveurs désagréables dans l'environnement aquatique

Ce colloque se tiendra à Espoo, dans la banlieue de Helsinki (Finlande) du 14 au 18 juin 1982. Il est patronné par l'*International Association of Limnology* et divers organismes nationaux finlandais, y compris la Société limnologique finlandaise et l'Association de l'eau de Finlande.

La plupart des aspects des problèmes de saveur (odeur et goût) dans l'eau et les organismes aquatiques (psychophysique, chimie, biologie et technologie) seront traités au cours de ce colloque.

Pour plus d'information, on est prié de communiquer avec l'une des personnes suivantes : *Dr Taina Kuusi, Secrétaire du colloque, Centre d'État de recherches techniques, Laboratoire de nutrition, Biologinkuja 1, SF-02150, Espoo 15, Finlande;* ou *Dr Per-Edvin Persson, Président du comité du programme, Université de Helsinki, Département de limnologie, Viikki, SF-00710, Helsinki 71, Finlande.*

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia **W. G. Wharton and K. H. Mann**

Radiotracer experiments on phosphorus uptake and release by limnetic microzooplankton **W. D. Taylor and D. R. S. Lean**

Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors **K. T. Frank and W. C. Leggett**

Uptake of waterborne methylmercury by rainbow trout (*Salmo gairdneri*) in relation to oxygen consumption and methylmercury concentration **D. W. Rodgers and F. W. H. Beamish**

Aeromonas salmonicida: relationship between extracellular growth products and isolate virulence **R. C. Cipriano, B. R. Griffin, and B. C. Lidgerding**

Elimination of hexachlorobenzene (HCB) by rainbow trout (*Salmo gairdneri*) and an examination of its kinetics in Lake Ontario salmonids **A. J. Niimi and C. Y. Cho**

Developmental responses of juvenile *Daphnia rosea* to experimental alteration of temperature and natural seston concentration **W. E. Neill**

Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management **J. A. Gore and R. D. Judy Jr.**

Twilight activities and temporal structure in a freshwater fish community **G. S. Helfman**

Initial colonization of artificial substrate: community development and structure studied by scanning electron microscopy **C. Hudon and E. Bourget**

Physical control of phytoplankton production under sea ice (Manitounuk Sound, Hudson Bay **L. Legendre, R. G. Ingram, and M. Poulin**

The effect of phosphorus limitation on algal growth rates: evidence from alkaline phosphatase **R. E. H. Smith and J. Kalff**

Production responses for multi-species fisheries **R. J. Agnello and L. G. Anderson**

The structure of crustacean zooplankton communities in glaciated eastern North America **J. C. Roff, W. G. Sprules, J. C. H. Carter, and M. J. Dadswell**

Larval and juvenile stages of the isopod *Holophryxus alaskensis* (Epicarida, Dajidae) parasitic on decapods **K. O. Coyle and G. J. Miller**

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Influence of substrate composition and suspended sediment on insect predation by the sculpin *Cottus rhotheus* **M. A. Brusven and S. T. Rose**

Distribution tissulaire du cadmium chez *Meganyctiphanes norvegica* (euphausiacée) : état naturel et accumulation expérimentale de formes solubles **L. Poirier et D. Cossa**

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Stock assessment and life history of a newly discovered Alaska surf clam (*Spisula polynyma*) resource in the southeastern Bering Sea **S. E. Hughes and N. Bourne** 1173–1181

Hemoglobin levels and red cell ionic composition in goldfish (*Carassius auratus*) exposed to constant and diurnally cycling temperatures **T. F. Koss and A. H. Houston** 1182–1188

Parr–smolt transformation of yearling Atlantic salmon (*Salmo salar*) at several rearing temperatures **C. E. Johnston and R. L. Saunders** 1189–1198

A procedure for evaluating the food biomass consumed by a fish population **J. Majkowski and K. G. Waiwood** 1199–1208

An in situ study of cadmium and mercury stress in the plankton community of Lake 382, experimental lakes area, northwestern Ontario **J. S. Marshall, J. I. Parker, D. L. Mellinger, and S. G. Lawrence** 1209–1214

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